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On a quest for understanding anger: The influence of trait anger on risk attitudes and neural correlates of anger as a stimulus evoked affective state

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ABSTRACT

Anger is commonly referred to in the context of aggressive behaviors. However, little is known about more nuanced effects of this emotion on behavior, nor its neural correlates as a subjective feeling state. For instance, several studies suggest that angry people, in contrast to anxious individuals, perceive risks optimistically. It remains unknown whether these opposing effects of trait anxiety and trait anger on risk perceptions manifest in a direct behavioral measure of risk taking. Our first experiment showed, as predicted, that high trait anxiety was associated with pessimism, whereas anger exerted an optimistic bias on likelihood perceptions. However, these biases did not translate into differences in risk taking behavior. Instead of optimism, impulsivity was highlighted as a mediator of risk proneness in individuals who tend to express anger. A second project investigated the neural basis of anger as an affective state elicited by emotionally evocative social scenes. Participants' attention was directed towards transgressors or their victim, which elicited feelings of anger and sadness respectively. These distinct emotions were associated with differential activity patterns in regions related to affective processing; the amygdala, insula and subgenual anterior cingulate cortex. Individual differences in trait empathy emerged as strong modulators of these activity patterns. In contrast, the ventromedial prefrontal cortex response to transgressors versus victims correlated positively with an individual's tendency to express anger, suggesting a role of this region in the regulation of angry feelings.

RÉSUMÉ

La colère est couramment associée aux actes violents, mais nous connaissons mal l'effet plus nuancé de cette émotion sur le comportement, et les corrélats neuronaux de cet état affectif restent à préciser. Par exemple, plusieurs études suggèrent que les personnes colériques, à l'opposé des personnes anxieuses, sont plus optimistes face à un risque. Il n'est toutefois pas clair si ces effets contraires se manifestent par des mesures directes du comportement lors de la prise de risque. Notre première étude montre, qu'une prépondérance du trait d'anxiété est associée au pessimisme, alors qu'un trait colérique entraîne un biais optimiste sur la perception de la probabilité du risque. Cependant, ces biais ne se traduisent pas par des différences comportementales face au risque. L'impulsivité, plutôt que l'optimisme, s'est démarquée comme variable modératrice de la disposition à prendre un risque chez les individus aux traits colériques. Un second projet à explorer les corrélats neuronaux de la colère en tant qu'état affectif suscité par des scènes sociales émotionnellement évocatrices. L'attention des participants était dirigée vers un transgresseur ou sa victime, suscitant respectivement des sentiments de colère ou de tristesse. Ces différentes émotions étaient associées avec des patrons d'activité cérébrale distincts au cœur des zones liées au traitement affectif : l'amygdale, l'insula et le cortex cingulaire antérieur subgénual. Les différences individuelles sur le trait d'empathie ont exercé une forte influence modératrice sur ces patrons d'activité. En contraste, la réponse du cortex préfrontal ventromédian aux transgresseurs (contrasté à la réponse aux victimes) a positivement corrélé avec une disposition colérique, suggérant un rôle de cette région dans la régulation de sentiments colériques.

General Introduction

Anger or mild annoyance is part of everyone's daily emotional experience. Life is full of events that trigger this emotion, may it be a car that cuts into traffic, a boss who makes a degrading remark or a romantic partner who openly flirts with an attractive stranger at a party. In the short or long run everyone is caught up by this unpleasant emotion and often time people fail to use their anger constructively.

Whereas research throughout the last decades has largely advanced our knowledge of the effects of anxiety and depression on behavior and cognition, anger has been lagging behind starting with the absence of a commonly accepted definition of this construct. To date, opinions in the research community collide on the precise characteristics of anger, its antecedents and its consequences. Nevertheless, research has succeeded in identifying a common ground of general attitudes, behaviors and eliciting events that clearly differentiate anger from other negative emotions. Capturing the moral tone inherent to anger, Averill's findings showed that the perception of a voluntary injustice or a potentially avoidable accident is a characteristic that marks 82 % of the anger experiences reported (Averill, 1982). As a consequence, angry individuals usually tend to perceive their emotional responses as justified, which jointly with their tendency to ruminate and nurture thoughts of revenge (Fitzgibbons, 1986; Sukhodolsky et al., 2001), might explain their relatively small motivation to change or control their angry feelings (Scherer & Wallbott, 1994). As Scherer and Wallbott (1994) in a cross cultural study of the phenomenological experience of emotions noted, the only emotion that individuals are less inclined to control is joy. Contrary to fear, anger is thought to require an attribution of agency followed by an outward projection of blame towards the cause of the perceived misdeed, (Clore & Centerbar, 2004; Scherer, 2001)but see (Berkowitz & Harmon-Jones, 2004) for a different view. As such we usually get angry at someone. Given that this projection may neither be rational nor correct, our anger is quite likely to hit the wrong person (Clore & Centerbar, 2004). Indeed, anger, particularly when experienced frequently, has a detrimental effect on our social relations (Scherer & Wallbott, 1994; Tafrate et al., 2002) and our vocational success (Gibson & Barsade, 1999). Whereas fear is closely linked to harm avoidance and withdrawal behaviors, anger is the only negative emotion associated with an increased likelihood to approach the eliciting event (Scherer

& Wallbott, 1994). Particularly the approach tendency of anger and its action readiness towards the cause of the perceived misdeed, might be the most distinguishing characteristics that separate this emotion from other negative affective states such as fear or sadness. The expression of anger in form of physical or verbal aggression constitutes an outwardly impulsive response. It is therefore of little surprise that researchers have found positive relations between anger and impulsivity (Milligan & Waller, 2001; Ramirez, 2006).

Given the different motifs ascribed to anger and fear, it follows naturally to hypothesize that they will exert distinct if not even opposite effects on behavior and cognition, which in turn will be reflected in different patterns of brain activation. Indeed, whereas anger alike to happiness has been associated with enhanced left prefrontal activity, fear and sadness have been linked to increased right prefrontal activity (Harmon-Jones, 2007; Harmon-Jones & Allen, 1998). A divergence between these two emotions has also been found in terms of risk perceptions. Whereas angry individuals tend to perceive their risks optimistically, the opposite has been reported for anxious individuals (Fischhoff et al., 2005; Lerner & Tiedens, 2006).

Sate versus Trait Anger

When investigating the effects of anger on behavior or its neural correlates it is important to distinguish between anger as a transient emotional response to a specific situation and the general disposition of an individual to experience anger. The prior one, is referred to as state anger and is associated with momentary physiological and autonomic arousal as well as muscular tension that prepares the body for action. These bodily responses cease down to baseline again once the specific situation is resolved. Trait anger in contrast refers to an individual's general disposition to experience states of anger across different contexts and situations. Individuals high in trait anger have a general propensity to interpret events in their surroundings as threats to their ego and values. As a consequence they are triggered into states of anger more easily and more frequently than others (Deffenbacher et al., 1996). Their anger in response to minor incidences is often exaggerated and their attribution of blame habitual rather then justified by a specific cause. Particularly the outward projection of blame makes angry individuals not only a danger to themselves but also to their social surroundings. Whereas state anger when applied constructively is adaptive in that it helps individuals to deter threats to their person and resolve conflicts, elevated levels of trait anger are dysfunctional. They come along with hostile and antagonistic attitudes that will impair an individual's well being, social life and general functioning.

Anger the "Forgotten Emotion"?

Given the lack of attention to anger by the general scientific community starting from psychology textbooks to techniques for anger resolution (DiGiuseppe & Tafrate, 2007; Kassinove, 1995), several researchers have given anger the ungraceful name of a "forgotten emotion". However, researchers may not have forgotten this emotion but instead may have lacked the means to step up and study this complex construct. The following paragraphs highlight the difficulties of the research community in studying anger and describe reasons for the slow advancement in this field.

As mentioned previously, researchers still struggle in finding a commonly agreed definition of anger. In turn, a construct that is not clearly defined is hard to measure. This might be one reason why the literature on the assessment of anger is so sparse. Strengthening this argument with numbers, from 1971 to 2005, 1,081 articles were published on the assessment of depression, 744 on anxiety and only 74 on the assessment of anger (DiGiuseppe & Tafrate, 2007). The most widely used scale to assess anger in the healthy population is the Spielberger state and trait anger scale (STAXI-II) (Spielberger, 1999). Since opinions of inherent characteristics and dimensions of anger are controversial, there are still ongoing arguments that this measure might miss out on important aspects of anger such as for instance rumination. Nevertheless, the good psychometric properties and the decent test-retest reliability (r values range from 0.70 to 0.77, Jacobs et al., 1988; Morris et al., 1996) of the STAXI-II highlight this measure as a valuable tool and good starting point for current research to measure the construct of anger.

Secondly, anger is extremely difficult to study in laboratory settings. Whereas fear can be easily investigated in classical conditioning paradigms that present individuals with an aversive noise or an electric shock, anger is differentially harder to elicit naturally.

It generally involves the violation of someone's rights or values. For obvious ethical reasons this is hard to implement in a laboratory. Furthermore, inducing anger naturally is not only unpleasant for the participant but usually also for the experimenter who has to handle this person. To circumvent these problems, the vast majority of studies that investigated the effects of anger on performance in behavioral tasks induced angry mood states by means of autobiographic mood induction. Mood induction based on recall of angering life event bears the disadvantage that participants may provide the behavior and responses that they believe are expected of individuals in angry moods, in particular psychology students. The difficulty of measuring the effect of state anger on behavior in an ecologically valid way is no reason to drop anger as an emotion out of one's research. One may for instance instead investigate how trait anger, that is an individual's general propensity to feel angry, shapes behavior and judgments. Several recent studies adopted this approach to investigate the effects of anger on attention biases and judgments (Lerner & Keltner, 2000, 2001). This approach is also implemented in the first project of the current thesis which investigated the influence of trait anger on risk attitudes.

Thirdly, research hindered an advancement of the understanding of anger by failing to differentiate the construct of anger from aggression. Indeed, aggression is one out of many behavioral reactions that may follow states of anger, but it is neither essential for its experience nor a necessary consequence of anger. Physical aggression in response to anger eliciting events appears to be a quite rare incident, occurring in only 10% of the anger episodes reported (Kassinove et al., 1997). By narrowing the scope of research to reactive aggressive behaviors one will not only miss out essential components of the emotional experience of anger, but also more subtle effects of anger on behaviors; such as for instance on attention or memory related processes. Investigating these effects is critical to develop a more comprehensive understanding of this emotion.

As the above paragraphs illustrate, researchers are slowly turning their heads towards anger and venture to fill the gaps of this previously "avoided emotion". Of particular interest to the current thesis are two aspects of anger: Firstly, the influence of anger as an emotional trait on risk attitudes, and secondly, the neural correlates of anger as an emotional state. The below paragraphs briefly highlight the present standing of research on these topics followed by a short introduction to the projects of this thesis.

Anger and Risky Decision Making

Apart from triggering aggression, anger may influence our behaviors and attitudes in more subtle, but equally important ways. Particularly, anger has been proposed to dangerously alter our perceptions of risk (Lerner & Tiedens, 2006). Importantly the influence of anger on the evaluation of risk is not constrained to emotional states, but extends to anger as an emotional trait. For instance, research has shown that individuals high in trait anger report overly optimistic expectations of personal future life events across various domains comprising health and vocational contexts as well as in interpersonal relations (Lerner & Keltner, 2001). This exaggerated optimism stands in marked contrast to their real life experience and has thus been suggested to tempt them towards risky choices (Lerner & Keltner, 2001). The major body of work so far has investigated the influence of anger on risk attitudes by means of self report measures, particularly in form of subjective probability estimates. Next to the general weaknesses of self report measures (e.g. lack of insight into one's behavior), perceived subjective probabilities are not the only determinants of our choices. For instance, an enhanced perception of the severity of potential losses usually prevents individuals in happy mood states despite their optimistic likelihood perceptions from undertaking risks (Isen et al., 1988). In addition, self-report measures that demand participants to rationalize their risk preferences may fail to capture a direct influence of anger on risky choice behavior that evades cognition (Loewenstein et al., 2001). Particularly, it has been hypothesized that the approach motifs associated with anger may tempt participants towards outwardly impulsive behaviors (DiGiuseppe & Tafrate, 2007). This suggests that angry individuals may engage risky behaviors independently of a rational choice process, but based on their tendency to act impulsively. Therefore the relation between anger, risk evaluation and decision making merits further attention, particularly with the aim of identifying whether and under which conditions anger translates into risky decision making.

The Neural Basis of Anger

Whereas a multitude of studies engaged in delineating neural correlates of fear, paucity of functional imaging research addressed anger. Several PET studies investigated the neural basis of anger by means of autobiographic mood induction. Regions implicated in the experience of anger are not consistent across studies. Whereas Damasio and colleagues (2000) next to other regions, reported activation of the insula, none of the remaining PET studies yielded support for an involvement of this region in the experience of anger (Dougherty et al., 2004; Dougherty et al., 1999; Kimbrell et al., 1999). Concerning, prefrontal activations, Damasio and colleagues (2000) reported a significant deactivation in the orbitofrontal cortex. In contrast, Dougherty et al. (1999) found increased activation in the left orbitofrontal cortex, followed by left ventromedial prefrontal cortex activation in a subsequent study (Dougherty et al. 2004). Interestingly, none of these studies reported significant amygdala activation when contrasting brain activity in angry mood states with neutral affect. The amygdala, next to ventromedial and orbitofrontal regions, has been identified as a key structure in emotion processing (for meta-analysis, see Sergerie et al., 2008). PET studies may lack the temporal resolution to pick up a potential involvement of the amygdala, as evidence indicates that activation in this region in response to triggering stimuli may be more transient. Furthermore, mood induction paradigms entail several confounding processes such as episodic memory retrieval and mental imagery that offer little experimental control regarding the precise timing, contextual experience and emotional intensity of the imagined scenarios across participants. Hence differences in brain activation might be the result of differences in any of these confounding variables across conditions rather than anger itself. In order to delineate the neural basis of anger it is of necessity to study anger as a stimulus evoked affective state (e.g. by using anger eliciting pictures) with imaging techniques that have a higher temporal resolution, such as for instance fMRI.

<u>On a Quest for Understanding Anger: Projects of this Thesis</u>

The first part of the current thesis focuses on anger as an emotional trait. In particular it investigates how this general interpretational bias influences an individual's optimism, risk attitudes and risky decision making. As previous research has shown, trait anger does not only shape an individual's reactions to and appraisals of anger triggering events, but penetrates into judgments of seemingly unrelated issues (e.g. when judging one's probability of developing cancer) (Lerner & Keltner, 2001). Several previous studies employing self report measures of risk attitudes suggest that angry individuals, in contrast to anxious individuals, perceive risks optimistically and show an exaggerated optimism about their own future life events. To date, it remains unknown to which extent these optimistic risk attitudes translate into risky decision making in a behavioral measure of risk taking. The current research investigated this question and furthermore aimed at delineating the role of impulsivity as a potential moderator of relations between anger, optimism and risk taking.

The second project of this thesis focused on the neural correlates of anger, as an emotional state. Contrary to most previous research, which relied on autobiographic mood induction to elicit anger, the current fMRI study investigated anger as a direct response to anger evoking social pictures. The event related design together with the higher temporal resolution of fMRI compared to PET as an imaging method allowed to investigate an involvement of regions whose activation may be more transient.

Project 1: The Influence of Trait Anger on Optimism and Risk Taking

Background: Emotions, Risk Perceptions and Decision Making

Individuals differ in their tendency to take risks that is in their willingness to engage in activities that bear chances of harm. Whereas some experience excitement when thinking of the possibility of doing a parachute jump others feel extreme discomfort by the mere though of watching it. Risk is also experienced in less exciting activities, for instance when deliberating whether to invest our savings on the stock market or to leave them on standard saving plans, which promise only little increments but do not bear any chance of detrimental losses. Given the pervasiveness of risk in everyone's life and choices, it is of little surprise that researchers across multiple disciplines have long ventured to identify variables that would allow them to model and thus predict decisions under risk. From the early foundations of probability theory to recent models of expected utility theory (Luce & Weber, 1986; Schoemaker, 1982), the vast majority of traditional approaches to risk taking assumes that decision making is a cognitive process whereby individuals arrive at a choice by rationally weighting their options.

Factors such as emotions or stable personality characteristics received little attention by these theories as they were not believed to be of relevance to the decision processes (for review, see Loewenstein et al., 2001). However, research throughout the last three decades has revealed that emotions in form of mood states or affective traits exert a strong impact on risk evaluations and ensuing choices. In a key paper Johnson and Tversky (1983) showed that a negative mood state, opposite to a positive mood, colors an individual's risk perceptions with pessimism. Importantly this pessimism prevailed throughout the set of events being judged independently of their relation to the source that triggered the mood in the first place. A finding that up to day has received wide support in the literature (DeSteno et al., 2000; Forgas, 1995; Mayer et al., 1992; Zelenski & Larsen, 2002).

Of particular interest to the present project, alike to mood states, emotional traits have also been shown to influence an individual's risk attitudes (Maner & Schmidt, 2006; Zelenski & Larsen, 2002). Contrary to transient mood states, emotional traits exert a stable influence on an individual's perceptions and evaluations of his or her surroundings.

This influence penetrates into risk perceptions and is at least in part independent of an individual's current mood (Gasper & Clore, 1998; Zelenski & Larsen, 2002).

Angry Optimists and Anxious Pessimists

Recent findings suggest that the influence of negative affect on risk perceptions is unlikely uniformly pessimistic but is instead specific to the emotion at hand (DeSteno et al., 2000; Lerner & Tiedens, 2006). That anger and fear might influence risk attitudes differently, if not even in opposite directions, becomes particularly evident when considering their distinct functional roles. Fear and anger evolved to implement distinct and specific functions. Both are part of a natural defense system that in response to imminent threat or danger initiates the "fight-or-flight" response (Cannon, 1914). Fear, as a defensive response to threat, motivates escape and avoidance behaviors to minimize harm. Conversely, anger, as the offensive counterpart, primes aggression and motivates approach behaviors aimed at deterring the threat (Frijda, 1986). Based on the different motives and functional roles associated with anger and anxiety, it has been hypothesized that angry individuals, contrary to anxious individuals, would undertake the threat of a risky prospect (Fessler et al., 2004).

Switching from evolutionary accounts of emotions, to a different theoretical framework namely appraisal theories, the factor analytic work of Smith and Ellsworth (1985) defined anger as an emotion that derives from the perception of high certainty and control. In contrast, fear is associated with the perception of uncertainty and lack of personal control (Smith & Ellsworth, 1985). In turn, the belief that a situation or a hazard is under personal control and thus to a certain degree manageable reduces its perceived risk (Peters & Slovic, 1996). Motivated by these theoretical accounts and in particular the work of Smith and Ellsworth (1985), Lerner and colleagues conducted a series of studies in which they pursued the hypothesis that anger with its appraisals of high control and certainty would bias angry individuals towards overly optimistic risk perceptions and risky choices. Results confirmed their hypothesis: Individuals high in trait anger relative to individuals high in dispositional fear/anxiety indicated optimistic risk perceptions of annual fatalities in the US across a range of negative events (stroke, floods, cancer) and made risk seeking choices in a hypothetical scenario (Asian Disease Problem, Tversky &

Kahneman, 1981) (Lerner & Keltner, 2000, 2001). Confirming that the optimism of anger extends to events of direct personal relevance, elevated levels of trait anger (and trait happiness) were associated with overly optimistic likelihood judgments of experiencing various positive and negative future life events (e.g. having a heart attack before the age of 50) (Lerner & Keltner, 2001). In contrast, high scores in a composite measure of dispositional fear/trait anxiety were consistently associated with pessimistic likelihood perceptions and with risk avoidant choices in the hypothetical scenario (Lerner & Keltner, 2000, 2001).

Subsequent studies turned away from emotional traits and instead investigated the influence of anger and fear on risk attitudes in form of mood states. Consistent with their theoretical predictions, Lerner and Keltner (2001) identified that appraisals of control mediated the opposite effects of anxious and angry mood states on expectations about future life events. Interestingly, reminding participants of their personal weaknesses and holding them responsible for the accuracy of their judgments could not completely eliminate the differences in optimism between anxious and angry individuals (Lerner & Gonzalez, 2005). Subsequent research confirmed and extended these initial findings by demonstrating that angry and fearful mood states exert opposite effects on risk appraisals, which may even retrospectively bias memories of perceived risk (Fischhoff et al., 2005; Lerner et al., 2003). This set of results suggests that in angry individuals, optimism about prospective outcomes leads to risky behaviors, whereas in anxious individuals, pessimism leads to a bias towards safe alternatives (Lerner & Tiedens, 2006).

Anxiety and Risk Avoidance

Several findings are in accordance with the above proposed risk avoidant attitudes of anxious individuals. For instance, a recent study confirmed that high trait anxious individuals are not only pessimistic in their risk perceptions but are also less likely to engage in risk behaviors across a range of contexts (Maner & Schmidt, 2006). The risk avoidance of anxious individuals has also been shown in a behavioral measure of risk taking, the Balloon Analog Risk Task (BART; Lejuez et al. 2002) (Maner et al., 2007). While findings consistently replicate the tendency of high trait anxious individuals to estimate their own risk as higher compared to their peers (Maner & Schmidt, 2006; Mitte, 2007), the relation between trait anxiety and risk avoidant decision making is less stable. For instance, Mitte (2007) reported a positive relation between trait anxiety and risk avoidant choices in hypothetical scenarios depicting common everyday life situations in one sample, but could not replicate these findings in a subsequent sample using the same scenarios.

Inconsistent relations between trait anxiety and risk avoidance are also implied in two studies that used the Iowa Gambling Task or a slightly modified version of this paradigm (Peters & Slovic, 2000). In accordance with the notion that trait anxiety is related to risk avoidance, Peters and Slovic (2000) observed a negative relation between Behavioral Inhibition Scores (BIS-scores), a construct that is closely related to trait anxiety (Carver & Scheier, 1994), and choices from high-punishment decks (high wins and losses with net negative gain). In contrast, Miu and colleagues (2008) found high trait anxiety to be associated with impaired decision making in the Iowa Gambling Task by promoting risky decision making. High trait anxious individuals choose the risky high-punishment decks relative to the advantageous low reward decks (low wins and losses with net positive gain) significantly more often than low trait anxious individuals, resulting in overall poorer gambling performance. These results suggest that rather than consistently promoting risk avoidance, trait anxiety may interfere with rational decision making and prime individuals toward inconsiderate and potentially self defeating behaviors (Miu et al., 2008). Indeed Cooper and colleagues (2000) observed that high levels of neuroticism, a construct that is closely related to trait anxiety, either directly or in interaction with impulsivity predicted the engagement in health risk behaviors (Cooper et al., 2000). In line with these findings, positive correlations have been observed between trait anxiety and the engagement in health risk behaviors such as smoking initiation or substance use (G. C. Patton et al., 1998; G. C. Patton et al., 1996; Welte, 1985). However, findings across the literature are not consistent and the precise role of trait anxiety as a risk factor for health risk behaviors remains yet to be explored (Morissette et al., 2007).

In summary, several studies report associations between trait anxiety and risk avoidant decision making. However, failures at replication are common. Other research suggests that high trait anxiety, rather than priming risk avoidant choices, might interfere with rational decision processes, thereby motivating inconsiderate and self defeating risky behaviors.

Anger, Optimism and Risk Taking

Evidence associating anger as a mood state and personality trait with optimism and risk proponent attitudes appears pervasive. Although Lerner (2006) advocates that such relations are uncontroversial, inconsistencies haven been reported in the literature. In contrast to the literature on risk taking, studies investigating the relation between anger, health and general life satisfaction have reported negative correlations between trait anger and dispositional optimism (Comunian, 1994; Puskar et al., 1999). In particular, high trait anger and anger expressivity have been associated with pessimistic life attitudes, whereas the control of angry feelings (e.g. by cooling off or calming down) has been positively correlated with optimistic life expectations (Puskar et al., 1999). It should be recognized that measures of situational optimism ask participants to judge the likelihood that they will experience a set of specific life events as compared to an average peer (e. g. "I developed a drinking problem", Weinstein, 1980), whereas dispositional optimism captures an individual's general expectation that good rather than bad events tend to happen (e.g. "In uncertain times, I usually expect the best", Scheier & Carver, 1985). A potential explanation for the controversial findings for anger and optimism might be that situational optimism relates more closely to risk perceptions than dispositional optimism. The two measures of optimism may thus capture slightly different constructs which in turn relate differentially to anger. In support of this explanation, dispositional and situational optimism appear to be related only moderately (Radcliffe & Klein, 2002; Taylor et al., 1992). However a different and equally appealing explanation might be that differences in the statistical analyses applied underlie these controversial findings. Trait anger and trait anxiety are usually moderately strong and positively correlated (Lerner & Keltner, 2001; Spielberger, 1999; Van Honk et al., 2001). This indicates that individuals who are angry more often are also more anxious. Motivated by appraisal theories of emotions, Lerner and Keltner (2000, 2001) aimed to investigate whether anger and fear exert opposite and specific effects on an individuals risk attitudes. To achieve this goal, these researchers isolated the impact of trait anger on risk perceptions either statistically or experimentally by controlling for the influence of trait anxiety/fearfulness. Apart from Lerner and colleagues, to our knowledge, no other research group has isolated the effects of trait anger or trait anxiety on optimism or risk taking. Such an analysis might reconcile the controversial findings on the relation between trait anger and optimism. For instance, it might well be the case that alike to findings on dispositional optimism, trait anger is negatively correlated with situational optimism once the effects of trait anxiety are not accounted for. However, to date it is unclear whether differences in the constructs of situational and dispositional optimism or rather differences in the statistical or experimental methods applied underlie these controversies.

In addition, knowledge about the relation between trait anger and risky decision making in situations in which outcomes are of direct personal relevance is sparse. Of relevance to the complexity and cognitive nature of hypothetical scenarios or self report measures utilized in previous studies, recent theories of emotions and risk taking suggest that emotions may exert a direct impact on risky decision making which may even stand in conflict with cognitively based decision processes (Loewenstein et al., 2001). This suggests that emotions may play a far more prominent role in real life decision processes than in self report measures which force participants to rationalize their risk preferences. In order to fully capture the impact of incidental affect such as mood states or emotional traits on risk taking it is therefore essential to study the influence of these factors on risky decision making in behavioral tasks that alike to most real life decisions do not stress the cognitive aspects of the choice process. Consequently, traditional gambling or choice tasks which focus a participant's attention on probabilities might not be the optimal measure to capture these effects. Indeed it as been argued that the impact of incidental affect on risky decision making is best studied in paradigms that contain uncertainty; that is tasks that alike to most situations in real life do not explicitly state probabilities of respective choice options (Hockey et al., 2000).

Evidence that angry mood states may be related to increased risk taking in a behavioral task has been obtained by Fessler and colleauges (2004). In the behavioral task, participants choose between a sure pay off and a gamble of equal expected value, e.g. $15 as a sure payoff or a 40% chance to earn $37.50. Notably an effect of angry mood states on risky decision making was only found for males. As the authors mentioned themselves, these findings should be interpreted with caution as their behavioral measure of risk taking had several limitations. First, the internal consistency of choice behavior in the task was weak. Second, the task explicitly stated probabilities and thus emphasized cognitive processing, potentially reducing the impact of incidental affect on choice behavior (Hockey et al., 2000). Therefore this task potentially might not have been sensitive to a weaker effect of angry moods on risky decision making in females (Fessler et al., 2004). This illustrates a need for future studies in which the impact of angry moods on risky decision making as well as potential sex specific effects should be more firmly delineated. Furthermore, it remains to be explored whether trait anger is associated with risky decision making in a behavioral measure of risk taking.

Anger and Impulsivity

Supporting a positive relation between trait anger and the engagement in real world risk behaviors, Schroder and Carey (2005) observed that women high in trait anger engaged in more sexual risks. Interestingly, consistent with their risk behaviors, these women also indicated heightened HIV risk perceptions, that is they were relatively pessimistic when estimating their chances of contracting HIV. Furthermore, whereas heightened risk perceptions in low trait anger women motivated intentions to adopt precautionary behaviors, an opposite pattern was found for high trait anger women. High risk perceptions and HIV knowledge negatively predicted intentions to adopt protective measures. This irrational pattern of behavior in high trait anger women suggests that other variables rather than risk perceptions may underlie the engagement of angry individuals in real world risk behaviors. One candidate might for instance be impulsivity. By definition, impulsive individuals tend to act upon the spur of the moment without deliberation or foresight. When facing a risky prospect such individuals might engage in the respective activity without considering potential detrimental consequences. Indeed, impulsivity has been positively related to various risk behaviors such as gambling (Slutske et al., 2005), tobacco use (Baker et al., 2004), poly-drug use (Verdejo-Garcia et al., 2008) and sexual risk taking (Cooper et al., 2000). It has been hypothesized that particularly the approach motifs associated with anger jointly with the outward projection of blame might tempt angry individuals towards outwardly impulsive behaviors

(DiGiuseppe & Tafrate, 2007). A positive relation between trait anger and impulsivity is also confirmed by empirical findings in the literature (Ramirez & Andreu, 2006). This in turn suggests that angry personalities and particularly individuals who express their anger might engage in risky endeavors at least partially independent from a rational choice process, and thus optimistic likelihood perceptions, and primarily through their tendency to act impulsively. Impulsiveness should therefore be taken into account when investigating the relation between anger, risky decision making and the engagement in real world risk behaviors.

Weaknesses of Self Report Measures

Self report measures of risk attitudes have several limitations that illustrate the need of behavioral tasks to gain an ecologically valid understanding of an individual's risk attitudes (Lejuez et al. 2002). In particular self reports of risk behaviors are likely subject to a social desirability bias as engaging in behaviors that put oneself at risk for controllable outcomes (e.g. contracting a sexually transmitted disease) are negatively reinforced by society (Schroder et al., 2003). Next to this, and as a more general weakness of self reports, participants might lack insight into their past risk behavior or their general behavioral preferences (Schroder et al., 2003). In addition, prior exposure and experience with certain risk behaviors will differ across participants which in turn affects an individual's risk perceptions as well as subsequent engagement in risk behaviors (Sitkin & Weingart, 1995). For instance, some individuals might have been caught cheating in an exam, whereas others experienced benefits from it (i.e. did not get caught). Yet, others might have strong moral values that prevent them from engaging in ethical risks. In contrast, a behavioral task that is equally new to every participant eliminates the impact of personal history upon outcome expectations and choice behavior. Furthermore, unlike real world risk behaviors it is free of any moral or social context that instead of risk attitudes per se might shape an individual's choices. If indeed high trait anger individuals are optimistic in their likelihood perceptions and risk seeking as suggested by previous findings, then a behavioral measure even more readily then self report measures should pick up these effects. However, to date, it has not been explored whether these effects indeed hold true in a behavioral task.

Study Purpose and Rationale

The current research aimed at developing a more comprehensive understanding of the relation between trait anger, optimism and risky decision making. We first examined the relation between trait anger and situational optimism. Next, we investigated their relation to an individual's self reported tendency to engage in real world risk taking behaviors. In addition, the role of impulsivity as a potential moderator of these relations was examined. Our major interest was to investigate whether the risk proponent attitudes ascribed to high trait anger individuals in previous findings, would translate into risky decision making in a behavioral measure of risk taking. We choose to employ the Balloon Analogue Risk Task (Lejuez et al., 2002) for several reasons. First, the BART has been proven as a behavioral task of high ecological validity. Risk taking in the BART has been shown to be positively related to the engagement in various real world risk behaviors such as smoking, substance use and delinquent behaviors as well as to self report constructs of risk related traits, such as sensation seeking (Aklin et al., 2005; Lejuez et al., 2003; Lejuez et al., 2002). Second, and of particular importance given the proposed relation between anger and impulsivity, the BART appears to capture an aspect of risk taking that is distinct from mere impulsivity (Hopko et al., 2006; Hunt et al., 2005; Jones & Lejuez, 2005), but see (Lejuez et al., 2002) for different findings. Third, the BART contains aspects of uncertainty which has been proposed to be of importance when studying the impact of emotions on risk taking (Hockey et al., 2000). Contrary to many traditional tasks of risk taking, it does not explicitly state probabilities leaving it up to participants to learn and explore the task environment. Furthermore, the BART has recently been employed to investigate the relation between risk avoidance and trait anxiety (Maner et al., 2007).

Hypotheses

Based on previous literature on anger and risk attitudes, we hypothesized that trait anger would be associated with optimistic life expectations. Furthermore we hypothesized that trait anger would be positively correlated with an individual's tendency to engage in real world risk taking behaviors as well as with risky decision making in the behavioral measure of risk taking. Conversely, we hypothesized that high trait anxiety would be associated with pessimism and risk avoidant attitudes.

Methods

Participants

Participants in this study were 100 healthy volunteers (50 males and 50 females) who were recruited via McGill classifieds and postings on local universities and colleges. Recruitment ads were posted online on the McGill classifieds and on boards around several campuses (McGill, Concordia and Université de Montréal). The age range of participants was 18 to 27 years with a mean age of 21.2 years (SD=2.1 years). The experiment was approved by the Research Ethics Board of the Douglas Hospital Research Centre. In order to motivate participants to maximize their earnings in the behavioral measure of risk taking, they were informed at recruitment as well as prior to completing the BART that the precise compensation would be a function of their earnings in the task.

Measures

Anger: Trait anger (10 items) and anger expression and coping styles (32 items) were assessed with the respective components of Spielberger's State-Trait Anger Expression Inventory (STAXI-II) (Spielberger, 1999). In addition to trait anger, we entered the Anger Expression Index in the analysis. The Anger Expression Index quantifies an individual's overall tendency to express anger by computing the difference score among measures of anger expression and measures of anger control. This index is simply referred to as "anger expression" in the current paper.

Anxiety: An individual's tendency to experience anxiety was assessed by the trait component of Spielberger's anxiety scale (STAI-T) (Spielberger, 1983) and the neuroticism component of the NEO Five-Factor Inventory (NEO, FFI) (Costa & McCrae, 1992). The correlation between the two measures was strong ($r=0.97$, $p<0.001$). We therefore combined these measure into one index of dispositional anxiety by submitting all items to a principal component analysis and imposing a one factor solution that remained all items (eigenvalue = 10.98). The same computation was applied by previous research using similar measures (Lerner & Keltner, 2001). The standardized regression score for each participant was used as a composite index of dispositional anxiety/fearfulness.

Impulsivity: Impulsivity was assessed by the 40 item Barratt's Impulsiveness Scale (BIS) (J. H. Patton et al., 1995) and the 10 item impulsivity subscale of Cloninger's TCI Novelty Seeking component (Cloninger et al., 1991). The bivariate correlation between the two measures was strong ($r=0.68$, $p<0.001$). As in the case with anxiety, a combined index of impulsivity was computed by submitting the two measures to a principal component analysis and imposing a one factor solution that retained all items (eigenvalue= 8.33).

Optimism: We measured optimism by administering Weinstein's Measure of Optimism (1980) (Weinstein, 1980). In this self-report instrument, participants rate their perceived chances of experiencing specific future life events relative to the average same-sex students at their university. The items depict various positive and negative life events that could happen to students either in the near (e.g. getting one's car stolen) or more remote future (e.g. suffering a heart attack before the age of 50). Participants rated their likelihood of experiencing each life event along a visual-analog scale ranging from very much less likely over average to very much more likely. Ratings for negative life events were scored reversely. Subsequently, ratings were transformed to obtain values ranging from 4 (*very much less likely*) over 0 (*average*) to 4 (*very much more likely*) for easy comparison with previous studies.

Risk-taking: We administered the Domain Specific Risk Attitude Scale (DOSPERT) to capture an individual's tendency to engage in real world risk behaviors (Weber et al., 2002). This measure assesses risk taking in ethical (e.g., forging somebody's signature), health/safety (e.g., engaging in unprotected sex), recreational (e.g., going whitewater rafting during rapid water flows in the spring) and social (e.g., disagreeing with an authority figure on a major issue) contexts by 8 items in each context domain. Gambling (e.g., gambling a week's income at a casino) and investment risks (e.g., investing 5% of your annual income in a very speculative stock) are assessed by 4 items each. Since previous research challenged the validity of these distinct context domains (Maner & Schmidt, 2006) we decided to only report relations with the total risk taking score. Participants rate their likelihood of engaging in each risky activity on a 5-point likert scale raning from 1 = extremely unlikely to 5 = extremely likely.

Gambling Attitudes and Beliefs Scale (GABS): The GABS (R. B. Breen & Zuckerman, 1994; R. B. Breen & Zuckerman, 1999). contains 35 items that measure an individual's general beliefs, attitudes and affinity towards gambling. Ratings are collected on a 4-point scale ranging from strongly agree to strongly disagree. The GABS consists of one factor that captures an individual's general gambling affinity. Individuals with high scores on the GABS value gambling a social activity and find that their gambling success depends on luck as well as strategy.

Balloon Analogue Risk Task: The Balloon Analogue Risk Task is a computer-based behavioral measure of risk-taking. In the BART participants aim at maximizing their earnings by inflating computerized balloons. A detailed description of the task can be found in (Lejuez et al., 2002). In summary, the computer screen displayed a balloon that could be inflated by pressing a button on the keyboard. Each button press (= pump) increased the earnings for that balloon by 2 cents (the amount of money collected for this balloon was not displayed to the participant). Whenever desired, a participant could stop inflating the balloon by pressing another button. This transferred the money collected for this balloon to a participant's total earnings displayed on the screen and the next balloon appeared on the screen. When a balloon was pumped past a certain pre-determined point (see below), it exploded and the participant lost all the money collected for this balloon and consequently gained nothing in that trial. Three colors of balloons were presented. The probability of explosion for each balloon was uniformly distributed between 1 and 128, 32 and 16 pumps for blue, yellow and orange balloons, respectively. Participants were not informed that different balloon colors had different explosion probabilities. In total participants inflated 90 balloons. During the first 30 trials blue, yellow and orange balloons (10 of each color) were completed in an intermixed fashion. This intermixed presentation was followed by 3 blocks of 20 trials for each balloon color individually. This resulted in the following sequence of balloons: 30 intermixed trials, 20 yellow balloons, 20 orange balloons followed by 20 blue balloons. The experiment was run using E-Prime (Psychology Software Tools, Pittsburgh, PA). As in previous studies employing this task (Lejuez et al., 2002), we used the adjusted averages of pumps (i.e., excluding exploded balloons) for blue balloons as a measure of riskiness.

Procedure

All questionnaires were administered in computerized form using E-Prime (Psychology Software Tools, Pittsburgh, PA). Following the instructions of each questionnaire, each item was displayed individually on the screen with the corresponding response options below. There was no time limit for responses. Thirty eight participants completed all questionnaires on the same day. The remaining sixty two participants completed the risk questionnaire several months after the other measures (approx. 6 to 9 months). Including the testing date (same/delayed) as a group variable in the analysis did not change the pattern of results. In order to prevent biasing a participant's choices in the behavioral task, risk related self report measures were administered after completion of the BART.

Statistical Analysis

Bivariate correlations were computed in order to delineate interrelations among personality measures as well as their relation to BART scores. In order to statistically isolate the effect of specific interrelated personality measures on measures of optimism and risk taking, partial correlations were computed by means of multiple regression analysis. In these regression models interrelated personality measures (e.g. trait anger, trait anxiety and/or impulsivity) were entered simultaneously as predictors of the respective dependent measure of interest. This allowed us to investigate the individual contribution of each of these personality measures to the respective dependent measure by controlling for the variance explained by the other(s). To investigate whether present findings replicate prior research by revealing unrealistic levels of optimism among participants, one sample t-tests were computed which compared total optimism scores as well as optimism scores for positive and negative life events versus zero.

Results

Anger, Anxiety and Impulsivity

Trait anger scores in the current sample (see Table 1) were similar to normative data reported for a sample of similar age range (Spielberger, 1999). As expected, trait anger and anxiety were positively correlated ($r=0.29$, $p<0.005$). Significant bivariate correlations were also found between impulsivity and measures of trait anger ($r=0.23$, $p<0.05$) and trait anxiety ($r=0.30$, $p<0.005$). Furthermore, anger expression (AX-Index) correlated positively with trait anger ($r=0.54$, $p<0.001$), anxiety ($r=0.45$, $p<0.001$) and impulsivity ($r=0.49$, $p<0.001$).

Optimism

Total optimism scores (see Table 1), as well as optimism scores for negative and positive life events, were significantly larger than zero (all ps<0.001), indicating that participants judged themselves more likely to experience positive or to evade negative life events than the average same sex person at their university (their hypothetical comparison group). A negative correlation between trait anxiety and total optimism scores ($r=-0.35$, $p<0.001$) was found indicating that individuals with high levels of anxiety had pessimistic life expectations. Similarly, a negative correlation was observed between impulsivity and optimism ($r=-0.37$, $p<0.001$). Due to the significant correlations between anger, anxiety and impulsivity we proceeded to compute partial correlations by entering these variables simultaneously in a multiple regression analysis to predict optimism scores. This allowed to investigate the individual contribution of each of these variables to optimism by controlling for variance explained by the other two (see Table 2). Anxiety and impulsivity remained significantly negatively correlated with total optimism scores. In addition a trend for a positive relation between anger and optimism emerged (beta=0.16, $p=0.09$). Parameter estimates in the regression model were similar to values reported by Lerner and Keltner (2001) who investigated the effects of trait anger, anxiety and dispositional happiness on optimism (beta=-0.38 for anxiety and beta=0.13 for anger; (Lerner & Keltner, 2001)). This agreement with previous findings increased further, when, as in previous research, impulsivity was not included in the regression model (beta=-0.39 for anxiety, beta=0.12 for anger).

Concerning relations between expressional aspects of anger and optimism, we found a negative bivariate correlation between anger expression and total optimism scores ($r=-0.21$, $p<0.05$) indicating that individuals who tend to express their anger are relatively pessimistic. Subsequent analyses showed that this effect was mediated by impulsivity and/or anxiety.

Risk Taking

The average total score of the Risk-Taking Behaviors Scale across all participants (see Table 1) was similar to normative values ($M=2.8$, $SD=0.4$) reported by Weber and colleagues (2002) in a sample of students with a similar age range. Bivariate correlations yielded no significant relation between total optimism scores and an individual's willingness to engage in risk behaviors ($r=-0.06$, $p>0.52$). Examining the relation between risk taking and optimism for positive and negative life events separately yielded a significant negative correlation between optimism for negative life events ($r=-0.21$, $p<0.05$) indicating that individuals who engaged in real world risk behaviors were pessimistic about evading the experience of negative life outcomes. The correlation coefficient between positive life events and risk taking behaviors was positive, but did not reach significance ($r=0.13$, $p=0.19$). Since this pattern suggested that individuals who engage in risks expect themselves as more likely to experience negative as well as positive life events, we proceeded to compute the correlation between risk taking and the general expectancy of events to happen, may they be positive or negative. A significant positive correlation between the expectancy of events to happen and the tendency to engage in risk behaviors was observed ($r=0.27$, $p<0.01$). Furthermore, a strong positive correlation between impulsivity and an individual's willingness to engage in risk behaviors was found ($r=0.48$, $p<0.001$). Due to this, partial correlations were computed that controlled for the influence of impulsivity (see Table 3). The positive relation between the general expectancy of events to happen and risk taking persisted when partialing out the variance accounted for by impulsivity.

No significant bivariate correlations between trait anger, anxiety and risk taking were found ($r=0.05$, $p>0.62$ and $r=0.12$, $p>0.21$ respectively). This also applied to partial correlations in which trait anger, anxiety and impulsivity were entered simultaneously into a regression model to predict risk taking scores (see Table 4).

A significant positive bivariate correlation between the total amount of anger expression and a participant's tendency to engage in risk behaviors emerged (r=0.26, p=0.01). Subsequent analyses showed that this relation was mediated by impulsivity: When impulsivity and anger expression were entered simultaneously in a regression model to predict risk taking, the relation between anger expression and risk taking decreased to zero (see Table 5).

Balloon Analogue Risk Task: BART

The average adjusted number of pumps for blue balloons (BART score, see Table 1) was similar to values reported in a similar population of students (M=29.4, SD=13; (Lejuez et al. 2002)). For bivariate correlations between BART scores and personality measures refer to Table 6. BART scores correlated positively with the total risk taking score of the DOSPERT and general gambling attitudes and beliefs as measured by the GABS. Neither impulsivity nor optimism scores were correlated with risk taking in the BART. Furthermore, no significant bivariate correlations between trait anger, anger expression or anxiety and risk taking in the BART were observed. In order to isolate the effect of trait anger and anxiety upon risk taking in the BART, a regression analysis was performed and both variables were entered simultaneously as predictors of BART scores. These partial correlations did not yield any significant relations between these two emotional traits and risk taking in the BART (see Table 7).

Discussion

The present study extended previous research by investigating the relation between trait anger and risk attitudes not only by means of self report measures, but also in a direct behavioral measure of risk taking, the Balloon Analogue Risk Task (BART) (Lejuez et al., 2002). Furthermore impulsivity as a potential moderator of relations between anger, anxiety and risk taking was taken into account.

Anger, Anxiety and Optimism

As expected, trait anger and trait anxiety were positively correlated in the current sample. This confirms that individuals with elevated levels of trait anger also tend to be more anxious (Spielberger, 1999). Consistent with our hypothesis and previous findings, high trait anxious individuals were relatively pessimistic about future life outcomes. This is in agreement with general processing biases reported in the literature with regard to this trait. For instance, the tendency of anxious individuals to interpret ambiguous information as threatening or their increased sensitivity to signals of threat in form of attentional biases (Bradley et al., 1998; Eysenck et al., 1987).

Bivariate correlations yielded no support for an association between trait anger and optimism. However, as in previous research (Lerner & Keltner, 2001), a positive, albeit small, relationship between trait anger and optimism emerged when controlling for the influence of trait anxiety. It is important to emphasize that the positive association between trait anger and optimism was only observed in partial correlations that isolated the effect of each emotional trait on optimism and not in zero order bivariate correlations. Therefore, caution is required when drawing general conclusions about the life attitudes of high trait anger individuals. In real life, anger tends to co-occur with elevated levels of trait anxiety and does not have the isolated effect on optimism obtained in the current statistical analysis. Hence when individuals judge their likelihood of experiencing future life events, different traits of negative affect will combine in order to influence their judgments and the optimism ascribed to anger does not prevail (Zelenski & Larsen, 2002). This suggests that exaggerated optimistic life expectations are not expressed by angry individuals in general, as one might suspect based on the conclusions drawn by previous research, but by a subset of the population of angry individuals; namely those individuals who display elevated levels of trait anger and low levels of trait anxiety. Whereas this may have been indirectly implied by previous research, authors have not highlighted nor mentioned these limitations in their conclusions (Lerner & Keltner, 2001).

Consistent with the literature on dispositional optimism (Puskar et al., 1999), we observed a negative bivariate correlation between anger expression and optimism. Confirming the argument that concurrent high levels of trait anxiety might account for negative associations between anger and optimism, subsequent analyses showed that the pessimism of individuals who tend to express their anger is mediated by concurrent elevated levels of trait anxiety or impulsivity.

Impulsivity, Optimism and Real World Risk Taking

Impulsivity emerged as the strongest predictor of an individual's levels of optimism as well as of his or her willingness to engage in real world risk behaviors. Consistent with previous findings in the literature (Baker et al., 2004; Slutske et al., 2005), impulsive individuals were more likely to engage in real world risk behaviors. Furthermore, impulsive individuals were relatively pessimistic about future life outcomes suggesting that they are aware that their tendency to act without reflection or foresight is not associated with beneficial consequences.

Our results yielded no support for a positive relation between optimism and risk taking. Instead, they show that individuals who take risks believe that they are more likely to experience negative events as well as positive events. Hence, rather than being indiscriminate optimists, risk takers appear well aware that their tendency to engage in risky behaviors predisposes them to experience future harms next to potential benefits. This relative accuracy revealed by risk takers in the current study is consistent with results obtained in several studies on health and safety related risk behaviors, which reported that individuals who engaged in risk behaviors (e.g. smoking, risky driving, unprotected sex) also estimated their risks of suffering aversive effects related to these behaviors as higher (Otten & van der Pligt, 1992; Rutter et al., 1998). Importantly, these results highlight that direct conclusions from optimistic risk estimates on future life outcomes to increased risk taking tendencies are invalid. As a consequence this precludes direct inferences from the optimism ascribed to individuals high in trait anger to risk seeking attitudes.

Trait Anger, Anxiety and Risk Behaviors

We found no support for the hypothesized positive relation between trait anger and risk taking. This was the case for bivariate correlations as well as partial correlations that isolated the effects of trait anger on risk taking from anxiety and/or impulsivity. Instead of trait anger per se, the tendency to express anger correlated positively with real world risk taking. This highlights anger expression as a more useful predictor of an individual's willingness to engage in risky behaviors. Importantly, our results suggest that the risk proneness of individuals who tend to express their anger is not due to overly optimistic life expectations. Instead their readiness to engage in risky behaviors was mediated by their tendency to act impulsively. Hence, expressional aspects of anger rather than trait anger per se are more closely related to impulsivity and via this relation to the engagement in risk behaviors (e.g. cheating, unprotected sex).

Present findings yielded no support for an association between trait anxiety and risk taking. This is inconsistent with Maner and Schmidt (2006) who found that anxious individuals were risk avoidant. These authors employed the same self report measures of anxiety and risk taking as the current study, which negates the possibility that differences in measurements might account for this discrepancy. Inconsistent effects of trait anxiety on risk taking have also been reported by previous research, even when using the same paradigm (Mitte, 2007). The question is thus: which factors might explain these inconsistent findings?

The present results suggest that impulsivity is one factor that might account for the lacking risk avoidance of anxious individuals. Of interest, both trait anger and trait anxiety correlated positively with impulsivity in the current sample. This may appear surprising, given that impulsivity has been described as a construct that is orthogonal to trait anxiety (Barratt, 1993). Contrary to this point of view, a recent approach to impulsivity, the UPPS Impulsive Behavior Scale (Whiteside & Lynam, 2001), identified Urgency as a personality trait linked to neuroticism that captures an individual's tendency to act hastily under negative affect and to commit to behaviors in order to cope with or relieve their emotional distress even if haste action bears potential detrimental (long term) consequences. Hence the tendency to act on the impulse might direct anxious individuals to inconsistent, inconsiderate behaviors rather than towards steady risk avoidance.

Trait Anger, Anxiety and Risk Taking in the BART

Present results further validate the BART as a behavioral measure of risk taking. BART scores were positively correlated with the willingness of an individual to engage in real world risk taking. Consistent with several previous findings, we observed a positive correlation between BART scores and the GABS, but no correlation with impulsivity. This confirms that the BART captures an aspect of risk proneness that is distinct from mere impulsivity (Lejuez et al., 2003).

Contrary to our hypothesis we did not observe any associations between trait anger or trait anxiety and risk taking in the BART. This is consistent with present results obtained in self report measures of real world risk taking. Jointly, these absent relationships between anger, anxiety and risk taking provide strong support for no direct association between these constructs. Furthermore no relationship between anger expression and risk taking in the BART was observed. As mentioned previously, the tendency of individuals who express their anger to engage in risk behaviors was mediated by impulsivity. Given that risk taking in the BART was not associated with impulsivity it is thus not surprising that anger expression was no related to risk taking in the BART.

May social desirability biases account for these absent relations?

Several lines of evidence suggest that it is unlikely that social desirability biases accounted for absent relationships between anger, anxiety and risk taking in the present study. First, sample means in the risk behavior scale as well as in self report measures of emotional traits were close to normative means reported in populations of a similar age range and educational background. Consequently, if indeed a bias was present in the current sample, it was not different from biases commonly observed in this age group. One might expect that self reports of risk behaviors are particularly susceptible to social desirability biases, as engaging in sexual or ethical risk behaviors does not only endanger risk takers themselves but also violates moral standards of society or the well being of their peers. However, the present study was not constrained to self reports but included a behavioral measure of risk taking which eliminated or at least strongly reduced social biases by putting every participant in the same novel situation which was free of any personal history, social or moral context.

Limitations and Future Directions

The present study bears several limitations that need to be addressed by future research. Although we did not observe any sex interactions regarding associations between anger, anxiety and risk attitudes, the sample size might have lacked the power to delineate these effects. It is therefore necessary to further investigate potential sex specific patterns before any firm conclusions can be drawn.

Furthermore, recent evidence indicates that risk taking may differ across distinct content domains (Barsky et al., 1997; Hanoch et al., 2006). This means that individuals who take risks by gambling might not necessarily be recreational risk takers who enjoy bungee jumping. The present study did not report any domain specific effects because previous research had casted doubts on the validity of the content specificity of the domain specific risk behavior scale applied (Maner & Schmidt, 2006). Importantly, this does not preclude or argue against the possibility that risk taking varies across different contexts, but rather demands for the development of better self report measures to capture these effects. Thus, it remains to be investigated whether the effects of anger and anxiety on risk taking are dependent upon specific context domains.

Furthermore, and as is the case in the majority of studies in psychology, the present sample was more or less constrained to undergraduate students. Whereas this bears the advantage of reducing inter-subject variability in terms of educational background and socio-economic status; it has the disadvantage that present findings may not be extendable to other populations, such as elderly individuals. Once more, future research is required to investigate these associations in different populations.

Summary and Conclusion

Present findings confirm that trait anger and trait anxiety exert opposite effects on an individual's levels of optimism. Whereas trait anger was positively related to an individual's levels of optimism, the opposite was found for trait anxiety. However, present results do not suggest that these cognitive biases translate into risk proponent or risk aversive decision making in angry or anxious individuals respectively. Instead of emotional traits, impulsivity is highlighted as a strong predictor of an individual's levels of optimism as well as of his or her tendency to engage in real world risk behaviors. Moreover, the relationship between impulsivity and optimism was opposite to what one might expect. That is, impulsive individuals were relatively pessimistic about future life outcomes, suggesting that they are well aware that their tendency to act upon the spur of the moment does not necessarily yield beneficial outcomes. Furthermore impulsivity mediated the relationship between anger expression and risk taking, indicating that individuals who tend to express their anger engage in risk behaviors due to their tendency to act impulsively. This suggests impulse control rather than cognitive aspects of decision processes (e.g. likelihood perceptions) as a promising target for interventions that aim at reducing the risk behaviors of angry individuals.

Project 2: Neural Correlates of Anger

Originally it was planned to investigate the opposing effects of trait anger and anxiety on risk taking in an fMRI study. This would have allowed us to delineate neural correlates that underlie the different behavioral preferences of angry and anxious individuals. However, as we did not find any effects of trait anger or trait anxiety on risk taking behavior, we were forced to adopt a different approach. Instead of studying the effects of anger on behavior, we decided to conduct an fMRI study that investigates neural correlates of anger as a subjective feeling state. Of particular interest thereby was to delineate how anger, as a stimulus evoked affective state, differs from empathic concern for others.

Background: Neural Correlates of Anger and Empathic Concern

Anger and empathetic concern are social emotions elicited by our feelings towards and with other members of society. Anger is commonly experienced when our rights, interests or values are deliberately breached by someone else. As such, it usually involves an intentionally or recklessly caused unpleasant outcome followed by an outward projection of blame towards the agent responsible for our misery (Clore & Centerbar, 2004; Scherer, 2001). However, anger is not only experienced when our own interests are thwarted but also when the values and well-being of other members of society are deliberately violated. For instance, when the media report a severe case of abuse, society experiences strong empathic concern for the victims and conversely anger towards the offenders or advocates trying to cease their penalty (Raine, 1993).

Hoffman (1990) defined this form of anger as "empathic anger"; an empathy derived emotion experienced towards offenders at sight of a mistreated victim. Offenders, as targets of empathic anger, may be individuals, institutions or even nations whose actions deter the rights or well being of fellow human beings. Anger in this form may motivate and reinforce pro-social behaviors by evoking a desire to punish those who disregard others' interests (Vitaglione & Barnett, 2003). However, revenge seeking attitudes and hate, in particular when experienced intensely in light of severe offenses, may prevent us from improving the treatment of aggressors, as their imprisonment per se rather exacerbates than diminishes their criminal behavior (Raine, 1993). Consequently, developing an understanding of anger and empathic concern in terms of their triggers, their effects on subsequent behaviors as well as their neural basis has important implications not only for the individuals but also for the functioning of society. Only recently has research exposed aspects of the neural underpinnings of empathic concern and anger. In particular, the neural basis of anger as a subjective emotional experience remains poorly understood. Of particular interest to the current project is the extent to which anger towards offenders and empathic concern towards their victims differ at the neural level.

Emotions and Aggression: Key Regions

Anger alike to fear is usually triggered by a perceived threat, may it be to our own person or to our social surroundings. A key neural substrate implicated in the detection of emotionally salient information, threat as a prime example of this kind, is the amygdala (LeDoux, 2000). Whereas there is a vivid debate on whether or not the amygdala response to threat is automatic and independent of attention (Bishop et al., 2007; Pessoa et al., 2002; Pessoa et al., 2005; Vuilleumier et al., 2001), its role in the processing of emotional information ranging from basic fear conditioning to the evaluation of social cues in form of emotionally expressive faces is commonly agreed upon (Phelps et al., 2004; Sergerie et al., 2008). Its interactions with prefrontal regions, in particular the orbitofrontal and ventromedial prefrontal cortex (vmPFC), are thought to shape nuanced affective response and subsequent behavioral reactions (Davidson et al., 2000; Quirk & Beer, 2006). According to this model prefrontal regions exert a top down control on limbic structures such as the amygdala and by doing so regulate more instinctive fast paced emotional reactions based on the cognitive evaluation of a given situation. Support for this model has been obtained in form of inverse relations between prefrontal activations and the amygdala response or increased prefrontal activations per se when participants down-regulate their negative affective response to negative emotionally evocative stimuli (Levesque et al., 2004; Ochsner et al., 2004; Ohira et al., 2006; Urry et al., 2006). Confirming a critical role of ventromedial and orbitofrontal regions in shaping appropriate affective responses and behaviors, patients with lesions in these regions are impaired in recognizing social affective cues in form of emotionally expressive faces as well as in generating expectations about the emotional reactions of their surroundings, especially imminent angry reactions of their peers (Blair & Cipolotti, 2000; Heberlein et al., 2008). Once this limbic-prefrontal circuitry malfunctions, impulsive behaviors such as reactive aggression are likely to prevail (Coccaro et al., 2007; Davidson et al., 2000). In support of an involvement of prefrontal regions in impulsive aggression, a decade ago PET studies demonstrated diminished prefrontal metabolic activity in murderers pleading not guilty for reason of insanity relative to healthy controls (Raine et al., 1997). Extending these findings to other populations, a recent functional magnetic resonance imaging (fMRI) study showed an inverse coupling between the vmPFC and amygdala response to angry faces, as a basic signal of threat, in healthy controls (Coccaro et al., 2007). Strikingly, this coupling was absent in patients with intermittent explosive disorder, a disease marked by frequent impulsive aggressive reactions. Furthermore, across the whole sample, including healthy controls, the amygdala response to angry faces was positively correlated with prior aggressive behaviors. This suggests that an enhanced amygdala response to a perceived cue of social threat is not specific to clinically aggressive populations but covaries with individual differences in aggressive response tendencies in healthy individuals (Coccaro et al., 2007). It remains to be noted that although angry faces in the context of this study were referred to as signals of social threat (Coccaro et al., 2007), other researchers propose that a social threat is conveyed by embarrassing situations and social rejection rather than by signals of direct interpersonal aggression (e.g. angry faces) (Dickerson et al., 2004). In the framework proposed by Dickerson and colleagues (2004) social threat generally denotes a socially evaluative threat imposed to us by conditions in which our performance or behavior is subjected to the judgment of others. Yet, the term as employed by Coccaro and colleagues (2007) with reference to fearful or angry facial expressions may merely denote that a cue of imminent danger is conveyed to us by a fellow human being. One may suggest that both researchers attribute this term a different meaning. Furthermore, it is unlikely that participants experienced a strong subjective feeling state of anger in this imaging study, as angry faces per se do not provide a context of a perceived unfairness or blame which is usually required to trigger this emotion (Clore & Centerbar, 2004; Scherer, 2001) but see (Berkowitz & Harmon-Jones, 2004). Despite the fact that opinions on the precise nature of the term "social threat" or on essential preconditions (e.g. perceived unfairness) for anger might collide, these findings highlight that individuals with an increased tendency towards aggression reveal an enhanced amygdala response to cues of threat conveyed to them by other human beings. These cues of threat, per se, may not be enough to trigger anger but are a common constituent of situations that elicit angry or aggressive reactions.

Although these findings reveal deficiencies in general emotion circuits in reactive aggressive individuals, they provide little detail about regions implicated in the subjective experience of anger as an emotional state. Despite its relation to aggressive behaviors, the amygdala is unlikely the only player or sufficient to mediate the intensity and affective tone of the emotional experience of anger. For instance, electrical stimulation of the amygdala has been shown to reliably elicit negative emotional experiences such as fear or sadness as well as positive emotions, but only very infrequently anger (Halgren et al., 1978; Lanteaume et al., 2007). Indeed, prefrontal regions may play a more prominent role in higher order appraisals involved in anger, such as perceived violations of ones rights or interests compared to more basic and fast paced fear reactions to threat.

Neural Correlates of Angry Moods: Evidence from PET Studies

A series of PET studies has investigated the neural correlates of the subjective experience of anger by means of autobiographic mood induction (Damasio et al., 2000; Dougherty et al., 2004; Dougherty et al., 1999; Kimbrell et al., 1999). In these paradigms brain activation during the recall and re-experience of an angering event is compared to activation during the recall of a prior neutral life experience. Activation patterns observed in angry mood states are not consistent across studies. Whereas (Damasio et al., 2000) reported less activation during anger compared to neutral scenarios in the orbitofrontal cortex, others found an opposite pattern (Dougherty et al., 1999). Kimbrell and colleagues (1999) in turn reported increased activation in the left inferior prefrontal gyrus as well as in the left temporal pole. Only one study implicated an involvement of the insula in angry moods (Damasio et al., 2000). Dougherty and colleagues (2004) observed increased activation in the vmPFC during angry mood states. Although the amygdala was not significantly activated when contrasting angry mood states with neutral ones, its activation was found to be inversely coupled with the vmPFC response (Dougherty et al., 2004). This inverse coupling was absent in patients with major depressive disorder with anger attacks suggesting that a malfunction of this regulatory circuit might characterize this disorder (Dougherty et al., 2004).

In summary, evidence hints towards an involvement of ventromedial and orbitofrontal regions in the subjective experience of anger. However, findings across studies are not consistent, and the precise contribution of the amygdala and other limbic structures such as the insula are far from evident. In addition, mood induction entails several confounding processes that might account for the differential activation patterns observed across conditions. For instance, the semantic and social context might have differed between angry and neutral scenarios. In particular, anger usually involves a social context as typically we become mad at someone else. Neutral scenarios in contrast might have lacked this social tone. In addition, episodic memory retrieval as well as mental imagery might have varied across angry and neutral mood states. Furthermore, mood induction allows little experimental control of the precise timing and intensity of the emotional experience. Together with the weak temporal resolution of PET, this might have precluded the detection of regions whose activation is more transient, such as the amygdala. In order to draw more firm conclusions about the neural correlates of anger, it is necessary to study anger as a stimulus evoked affective state with imaging techniques that allow a higher temporal resolution such as fMRI.

Stimulus Evoked Anger: First Steps of Imaging Research

To date the stimulus evoked affective experience of anger remains relatively unexplored. Recently, an fMRI study reported increased activation in the dorsal anterior cingulate gyrus, the insula and middle medial prefrontal cortex following a direct interpersonal insult (Denson et al., 2008). Suggesting that the interpersonal insult succeeded in triggering states of anger in participants, activation in the dorsal anterior cingulate gyrus was positively correlated with self reported feelings of anger as well as with individual differences in general aggression. Interestingly, these researchers did not find evidence for involvement of the amygdala in this form of anger response. However, the interpersonal insult elicited other negative affects, such as guilt, making it difficult to time the precise second of the emotional response.

Stepping away from instigating anger by directly thwarting a participant's interests and feelings, a recent study on the neural basis of moral emotions reported activation of the left lateral orbitofrontal and insular cortices in response to imagined actions of another person that violated one's values (Zahn et al., 2008). A similar approach to instigate anger was adopted by (Harmon-Jones, 2007) in an EEG study. Angering images (e.g. Hitler, Ku Klux Klan), relative to neutral ones (e.g. neutral facial expressions), yielded increased left prefrontal activity that correlated positively with levels of trait anger. However, the anger eliciting images were not only differentially more arousing but also of higher semantic or historical content than neutral scenes, highlighting differential semantic and episodic memory retrieval processes as potential confounds. Furthermore, the well known inverse problem of EEG did not allow mapping of activity to discrete brain structures. These methodological weaknesses, as well as inconsistent results across studies, highlight the need to further explore neural correlates of anger in paradigms that control for these confounds.

Anger versus Empathic Concern

Advancing another step forward is to ask how anger differs from other moral or social emotions, such as compassion or sympathy for others. To date, research is stepping in the dark on whether these emotions are associated with different patterns of brain activation. Sympathy and compassion are constructs that reflect our feelings of sadness and concern towards an individual in emotional distress, physical pain or need. Their core is proximately related to empathy, which describes one's sharing of another's affective state, and in the converse case recognition that it is the source of one's distress or elation (Hastings et al., 2005; Preston & de Waal, 2002). Although, some researchers draw sharp distinctions between these two constructs (de Vignemont & Singer, 2006), they have a common base and may be grouped together into a broad class of related reactions that reflect our *Concern for others* (page 531, Hastings et al., 2000).

Recently Decety and Chaminade (2003) explored the neural basis of sympathy towards individuals in a state of sadness. While undergoing PET scans participants watched videos of actors portraying scenarios of sad, happy or neutral content with either matched (e.g. sad scene -sad expressions) or mismatched emotional expressions (e.g. sad scene - happy expressions). Watching actors depict sadness with congruent sad emotional expressions evoked high ratings of sympathy and was associated with activations in the left dorsal and left inferior prefrontal cortex, the lateral orbitofrontal cortex and temporal pole. These results are consistent with imaging studies on the neural correlates of sadness that used movie clips or autobiographic mood induction to induce sad mood states in participants. Commonly these studies reported activations in lateral orbitofrontal cortices, temporal poles as well as in the insula (Eugène et al., 2003; Lévesque et al., 2003a; Lévesque et al., 2003b; Pelletier et al., 2003). Hence these regions appear to be involved in establishing a state of sadness in individuals that may derive from reflecting upon their own previous life events as well as when observing others in distress.

Investigating empathy in a slightly different context, namely direct physical pain instead of solely emotional distress, (Singer et al., 2004b) reported that the insula and the anterior cingulate cortex are not only involved during the self experience of pain, but also when viewing others receiving painful stimulation. Activations were not constrained to the insula, but reached into the fronto-insular cortex and inferior prefrontal gyrus, particularly in the left hemisphere. Strengthening the role of the insula and the anterior cingulate cortex in empathic concern for others, brain activations in these regions were modulated by individual differences in trait empathy (Singer et al., 2004b; Singer et al., 2006). Furthermore, a subsequent study showed that empathy related activation in the insula depends on the perceived fairness of individuals undergoing painful stimulation, particularly for male observers. Instead of activating regions involved in empathic concern, such as the insula, when observing unfair players in pain males showed increased activation in a reward related region, the nucleus accumbens, that correlated positively with their desire for revenge (Singer et al., 2006). Indeed empathic concern and sympathy towards others may be seen as opposites to anger or closely related to revenge seeking attitudes.

In a recent study (Kedia et al., 2008) investigated whether these opposite emotions, compassion towards victims on the one hand and anger to transgressors on the other, are associated with different patterns of brain activation. Participants underwent fMRI scans while reading text vignettes of emotion evoking scenarios of self anger vs. guilt or other anger vs. compassion. Importantly, "other anger" in this study involved oneself as a victim (e.g. "my interests/goals are breached by someone") rather than focusing participants' attention on the transgressor of someone else. The direct comparison of other anger versus compassion yielded no significant activation differences, nor did comparisons between guilt versus other anger or compassion result in differential activation patterns. As the authors noted, one might expect these emotions to elicit different activations as they are associated with distinct subjective experiences and are triggered by opposite situations. The authors listed several methodological weaknesses that might have occluded potential activation differences. A weakness of text vignettes, as with general mood induction paradigms, is that they ask participants to mentally imagine scenarios. Such an indirect way of triggering affect likely results in variability across participants concerning the precise content of their mental and emotional experience and might thus preclude the detection of fine activation differences. Furthermore, the task did not ask participants to rate or engage in experiencing the predominant emotion evoked by the scenarios. This might have prevented a more differentiated emotional reaction to their content (Kedia et al., 2008).

Therefore, instead of merging anger and sympathy into the same neural substrates and/or activation patterns, these results highlight the need to explore more systematically possible activation differences between these two emotions. In particular, it has not yet been investigated whether anger towards an offender of someone else's well being differs from empathic concern towards the harmed victim.

Aims of the current study

The present fMRI study aimed to investigate the neural correlates of stimulus evoked anger and empathic concern to emotionally evocative social pictures that depict scenes of interpersonal transgressions (e.g. domestic violence, physical assaults). By focusing participants' attention and feelings towards the transgressor at one time, and to the victim of the same scene at another time, we aimed to delineate activation differences between anger and empathic concern given the exact same contextual background. A secondary aim was to examine to which extent individual differences in brain activation to transgressors versus victims correlate with emotional traits of empathy, anger and anger expression.

Hypotheses

We hypothesized that focusing an individual's attention to transgressors and victims of a scene would elicit different emotions, anger and sadness respectively, which would yield distinct patterns of brain activation. Anger tends to arise from events or persons that convey threat, whether they represent a threat towards society's norms and values or a threat of direct physical violence. We therefore hypothesized that the amygdala, would respond more strongly towards transgressors relative to victims, as they represent an imminent physical threat towards another individual's well being as well as to values common to every member of society. Given that in the present social scenes transgressors represent a threat that is more evolved than intrinsic cues of threat (e.g. fearful faces), we hypothesized that the amygdala response towards transgressors would be stronger when participants actively engage in relating their attention and feelings towards these persons. Several predominant theories of anger claim anger to be a differentially more cognitive and social emotion than fear in that it is associated with appraisals of perceived injustice and blame (Clore & Centerbar, 2004; Tavris, 1989). In line with these cognitive theories of anger we hypothesized that the reaction towards the source of threat in the form of an anger response would recruit regions such as the ventromedial prefrontal cortex, which have been associated with higher order emotional appraisals as well as with sustained angry mood states by previous research (Dougherty et al., 2004; Kalisch et al., 2006; Phan et al., 2005). Sadness or sympathy towards victims, in contrast, was hypothesized to be more closely related to activations in lateral inferior prefrontal regions (OFC) and temporal poles. Also of particular interest to the current study was to delineate whether anger or sadness/sympathy, which both have been associated with activations in the insula (Eugène et al., 2003; Zahn et al., 2008), would differ in terms of strength of activation of this region and/or recruit distinct parts of the insula. Since anger as elicited in the present paradigm has been referred to as "empathic anger", presuming that it arises from our caring for other persons (Hoffman, 1990), we hypothesized that individual differences in trait empathy would be most strongly related to brain activations associated with empathic concern (sadness) for others in distress as well as with anger towards their transgressors.

Methods

Participants

Twenty-three English speaking participants (Mean age: 21 years, Range: 18 to 28 years) were recruited at McGill University via advertisements on campus, online classified postings and by word of mouth. To assess present psychiatric illness or substance use/dependence, participants were screened by a clinical psychologist with the Mini-International Neuropsychiatric Interview (M.I.N.I.) (Sheehan et al., 1998). The M.I.N.I. is a widely used structured interview that allows for the screening of possible current and past life time DSM-IV and ICD-10 psychiatric disorders. This screening procedure resulted in the removal of two participants. None of the remaining 21 participants had previously been diagnosed with a neurological or psychiatric disorder. One participant met M.I.N.I criteria for past anorexia (> 1 year). Apart from this, no other undiagnosed past psychiatric illness including substance use/dependence was found. All of the participants were right-handed and had normal or corrected-to-normal vision. None of them had experienced a prior head injury with loss of consciousness nor were any currently taking any prescribed psychotropic drugs.

Ethics approval for all experimental procedures was obtained from the Institutional Review Board (McGill University, Faculty of Medicine). To ensure that participants were aware of the aversive content of the pictures prior to the MRI scan, they were asked to attend a brief meeting at the Montreal Neurological Institute. During the meeting participants viewed sample pictures, familiarized themselves with the task and provided informed written consent.

Stimuli and Task

Stimuli consisted of 30 pictures depicting social scenes of emotionally negative content (e.g. domestic violence, physical assault and sexual abuse) and 30 neutral to mildly happy control images (e.g. a couple shopping for clothes, a referee interacting with children in a soccer game). Common to all negative images was the depiction of a transgressor who violated the rights and well being of another human. Images were taken from the International Affective Picture System (IAPS) (Lang et al., 1997), commercial online picture databases, movies, and several other websources. The IAPS are a set of emotionally evocative color pictures that have been standardized and validated to be used in international experimental research on affective processes (Lang et al., 1997). IAPS images display a wide range of semantic and cultural contexts and have been applied in a multitude of imaging studies that investigated neural correlates of emotion processing. In order to minimize episodic memory retrieval, scenes that referred to specific persons or widely known historic events (e.g. World War II, Abu Ghraib prisoner abuse in Iraq) were avoided. Each negative image was matched with a neutral to mildly happy control image in terms of background content (e.g. a scene displaying domestic violence in an apartment was matched with a similar indoor scene), as well as the overall number and sex of persons present in the scene. As a result of the matching procedure, each transgressor had one corresponding control person in a control image (control person 1) and analogously each victim had one matched control person (control person 2).

The 60 images (30 negative, 30 matched neutral to mildly happy controls) were selected out of a large set of 180 images (60 negative images, 60 matched neutral controls and 60 matched mildly happy controls) in a separate behavioral experiment with a sample of 49 female participants (mean age=20.9 years, SD=2.9, age range=18 to 30 years). During this experiment, participants were asked to rate the predominant emotion they experienced towards the indicated person in a scene out of five target emotions (neutral, happy, fear, anger, sad). Arrows superimposed on each picture indicated the respective target person. Subsequently participants rated the intensity of the experienced emotion on a visual-analog scale ranging from "not intense at all" to "very intense". When a participant felt neutral towards the target person, no intensity rating followed. Each picture was presented randomly twice to every participant: once participants rated their feelings towards the transgressor (control person 1 for neutral or happy control images), the other time towards the victim (control person 2 for neutral or happy control images). To reduce the number of overall ratings, every participant rated all negative images and only one control scene for each negative image. Based on the frequency and intensity ratings of this pre-test we selected a subset of images that specifically induced the target emotions of fear and anger towards transgressors, fear and sadness towards victims and happy or neutral feelings towards persons in control images. In addition other selection criteria applied: Images were selected based on the semantic content of the scene to ensure that the final set did not contain a dominant theme. To assure that actors or movie scenes were unfamiliar to every participant in the MRI study, participants were asked to indicate films on a list of movies they had already seen. Images from two films that were known by several participants (10 and 8 participants respectively) were discarded from the final set.

As mentioned previously, for the fMRI experiment neutral and happy control images were combined resulting in 60 images: 30 negative images and 30 neutral to mildly happy matched control scenes. Neutral and happy images were combined for several reasons. First, combining these two a priori categories was necessary in order to reduce the number of stimuli for the fMRI paradigm. Second, boarders between happy and neutral images were not clear. For instance because in several scenes participants felt happy towards one person in a scene, but relatively neutral towards the other person. Furthermore, the content of neutral images was less engaging. Combining the two rather than constraining control stimuli to neutral social scenes thus reduced the possibility that differences between negative images and controls were driven by a differential engagement of participants towards the people in a scene.

Image Adjustments

Images were modified to achieve conformity between the sets of negative images and control images with respect to overall contrast, image quality, content, and intensity. To obtain similar contrast values and visual appearance between a negative image and its respective control image, sharpness, histogram functions and compression ratios were adjusted. In order to achieve consistency in image quality between negative images and their controls Gaussian blur filters (radius of 0.6 to 0.8 pixels) were applied to higher quality images. Finally images were mirrored to obtain similar person orientation in negative images and their controls.

Following these procedures the average contrast value for each image group (negative vs. control images), average overall color intensity and the average intensity for each color separately (R, G and B) were computed. Subsequently, the image intensity of control images was increased to achieve consistency with negative images. Adjustment for specific color tones (R,G,B) was not necessary because none of the image sets contained a dominant color tone. The adjusted intensity and contrast values for each set are displayed in Figure 1. One can see (Figure 1) that images in both sets are higher in R intensities. It is normal that R, G and B intensities are not equal within images. Usually, camera sensors absorb different wavelengths with different amplitude. Red color tends to be absorbed more easily and is therefore of higher amplitude (= intensity) on average. Finally independent sample t-tests uncontrolled for multiple comparisons were computed to compare image intensities and contrast values between the two sets. No significant differences were found (ps>0.5).

Personality Measures

Balanced Emotional Empathy Scale (BEES): The BEES (Mehrabian, 2000) was administered to measure individual differences in trait empathy. This 30-item measure of empathy consists of one factor capturing an individual's general propensity to vicariously experience the affective states of others as well as one's skill and empathic care in handling interpersonal relations.

Interpersonal Reactivity Index (IRI): The IRI (M. H. Davis, 1980) was administered as a second measure of individual differences in trait empathy. This 28-item questionnaire measures an individual's levels of dispositional empathy by means of four subscales: perspective taking (PT), empathic concern (EC), fantasy (FS) and personal distress (PD). The perspective taking scale captures one's propensity to adopt another person's point of view. The empathic concern scale measures one's tendency to sympathize and experience feelings of concern for others' in distress or need. The fantasy scale measures one's disposition to project oneself into fictional situations (e.g. when watching a movie) and the personal distress scale measures an individual's tendency to experience distress in emotionally charged situations, particularly in situations that depict others in physical or psychological distress.

Anger: Trait anger (10 items) and anger expression and coping styles (32 items) were assessed with the respective components of Spielberger's State-Trait Anger Expression Inventory (STAXI-II) (Spielberger, 1999). In addition to trait anger, we administered the

Anger Expression subscale that allows the computation of an Anger Expression Index. The Anger Expression Index quantifies an individual's overall tendency to express anger by calculating the difference score among measures of anger expression and measures of anger control. This index is simply referred to as "anger expression" in the current paper.

Anxiety: The trait component (20 items) of Spielberger's State-Trait Anxiety Inventory (STAI) (Spielberger, 1983) was administered to measure an individual's levels of dispositional anxiety.

Aggression: Individual differences in aggressive response tendencies were assessed with the Buss-Perry Aggression Questionnaire (Buss & Perry, 1992). This 29-item questionnaire comprises four subscales: Physical Aggression, Verbal Aggression, Anger and Hostility.

Trait Arousability: The abbreviated (14 item) version of Mehrabian's Trait Arousability Scale (Mehrabian, 1994) was administered to measure an individual's propensity to become aroused, that is to respond to changing or novel circumstances with increased levels of physical activity and alertness.

The administration of several scales related to empathy as well as anger served to assess the consistency of participants' scores across similar measures and to obtain an overall picture of the relation between these constructs. To reduce the number of variables in the correlational analyses between measures of trait affect and subjective emotion ratings as well as in the regression models applied to the fMRI data only a subset of these scales was employed.

The empathic concern component of the IRI (EC-IRI) as well as the BEES had been successfully employed by previous imaging research to measure individual differences in trait empathy and yielded correlations of similar strength within the same sample (Singer et al., 2004b; Singer et al., 2006). These two measures were highly correlated in the current sample ($r=0.63$, $p<0.005$). Furthermore, during behavioral piloting of the picture stimuli (sample = 49 females) positive correlations of similar strength between these measures and intensity ratings of sadness for victims were observed (r=0.49 for BEES and r=0.49 for EC-IRI, ps<0.001). Similar positive correlations also emerged for intensity ratings of anger towards transgressors (r=0.41 for BEES and r=0.57 for EC-IRI, ps<0.001). We therefore decided to only enter the BEES scale into the correlational analysis. The BEES scale was favored because its 30 items capture a broad dimension of empathic concern and caring about others compared to the fairly specific 7 item empathic concern subscale of the IRI. In addition, trait anxiety, trait anger as well as anger expression (AX-Index) were employed in order to assess, whether neural responses to negative scene content varied as a function of personality traits.

fMRI Data Acquisition

Data were acquired on a 1.5 Tesla Siemens Sonata Scanner with a standard head coil at the Montreal Neurological Institute. Stimuli were presented on a PC laptop with E-Prime (Psychology Software Tools, Pittsburgh, PA) and were projected via an LCD projector onto a screen viewed by participants through a mirror. Participants' responses were recorded by a two-button optical mouse connected to the laptop. Functional T2* weighted echoplanar images were acquired using blood oxygenation level dependent (BOLD) contrast (2 sessions of 240 to 260 volumes each, TR = 2450 ms, TE = 50 ms, FOV = 256 mm). Per image 30 axial slices were acquired in descending order parallel to the anterior-posterior commissural plane (voxel size 4 x 4 x 4 mm^3). A T1-weighted anatomical volume followed the two functional sessions (TR = 22 ms, TE = 9.2 ms, Flip angle = 30°, voxel size 1 x 1 x 1 mm^3).

Experimental Procedure (fMRI)

Prior to scanning participants completed the state component of Spielberger's anxiety scale. In addition they rated their current mood state on several dimensions on a visual-analogue scale: valence (*very unpleasant* to *pleasant*), arousal (*not aroused* to *very aroused*) and state anger (*not angry at all* to *very angry*).

Picture stimuli were divided into 2 sessions in order to give participants the chance to rest and thus reduce effects of fatigue during scanning. Each session consisted of 60 trials comprising 15 negative images (15 transgressor attended, 15 victim attended, 30 trials total) and 15 neutral to mildly happy control images (person 1 attended, person 2 attended, 30 trials total). During each presentation an arrow superimposed on the picture instructed participants to either attend and relate their feelings to the transgressor or to the victim (control person 1 or control person 2). In order to ensure that participants engaged in the task, they rated the experienced emotion towards the target person out of five basic emotion categories (Neutral, Happy, Fear, Anger, Sad) following each picture. See Figure 2 for an example of a trial.

Pictures were presented pseudo-randomly. Half of the images were attended towards the transgressor at first presentation and half of the images to the victim. In order to avoid the induction of a long lasting negative mood state no more than 3 negative images were presented consecutively. To prevent any habituation effects in either engaging towards the victim or transgressor of negative pictures, no more than two images that directly followed each other in the sequence were attended towards the same target person. In addition no two images of the same scene were presented consecutively.

Several sets of two sessions of picture stimuli were generated to minimize potential order effects. In each set the two sessions were balanced according to the content of the scenes, the image quality as well as the frequency and intensity of the experienced target emotions recorded during behavioral pre-testing. For the latter, intensity and frequency of ratings of each target emotion for each person category (transgressor, victim, control 1, control 2) from the behavioral pre-testing were evaluated using weighted t-tests (all $ps>0.1$).

After scanning, participants repeated the mood state ratings they completed prior to the scan. Subsequently pictures presented during the scan were presented once more. Participants indicated the predominant emotion experienced to each target person using the same interface as presented during the scan. They then proceeded to rate the intensity of the emotion on a visual analog scale ranging from "not intense at all" to "very intense". In case a participant felt neutral towards a target person, no intensity rating followed. Pictures were presented pseudo-randomly using the same ordering rules as during the scanning sessions. Following the emotion ratings, participants completed a package of personality questionnaires. For a detailed description of the personality measures applied, please refer to the Personality Measures subsection of the Methods.

fMRI Data Analysis

Images were analyzed with an event related general linear model using SPM2 (Wellcome Department of Imaging Neuroscience, London, UK). Prior to statistical analysis functional images were preprocessed: Images were realigned to the first volume and time corrected, normalized into standard space (final voxel size 2 x 2 x 2 mm) and spatially smoothed using a gaussian kernel with a full width half maximum (FWHM) of 8 mm. A high pass filter with a cut-off of 128s was applied to remove low frequency temporal drifts. Four event types of interest were specified: Transgressor attended, Victim attended, Control Person 1 attended and Control Person 2 attended.

Events were modeled with a standard synthetic hemodynamic response function with a boxcar length of 5 seconds starting at the onset of each picture. For each subject, six movement parameters obtained from the realignment procedure were included in the linear model as regressors of no interest in order to correct for residual effects of head movement. In addition to this analysis of primary interest (5 sec model), a second analysis was computed that modeled each image with a standard hemodynamic response function at the onset of each image (onset model). Rather than capturing sustained processes related to the active emotional engagement towards the target person that pertain throughout the whole duration of the image presentation (5 sec model), this second analysis aimed to capture activations related to the initial processing of the image content in regions that may only be transiently activated. Modeling events with a standard hemodynamic response function at the event onset with an overall duration of a fraction of a second is a commonly applied procedure in the analysis of event related designs and is implemented in SPM by entering 0 sec as the overall event duration (Huettel et al., 2004). The onset model, which models initial transient activity, was assumed to be better suited to detect activation differences in the amygdala as previous evidence indicates that responses in this region habituate quickly (Breiter et al., 1996). Although the temporal resolution of fMRI does not allow to examine activation sequences in the millisecond range, these two analyses nevertheless provide a crude approximation of initial versus longer lasting sustained processes.

To identify regions involved in the experience of anger relative to sadness contrasts were computed for each subject that compared brain activation to transgressors versus victims. In order to examine whether control persons for transgressors and victims were associated with differential activations, control person 1 was contrasted with control person 2. Furthermore, to isolate affective processes from activations related to the general engagement towards different persons in social contexts interaction contrasts of ([transgressor vs. control 1] vs. [victim vs. control 2]) were computed. These single subject contrasts were then entered into a whole-brain random-effects group analysis. Furthermore a conjunction analysis [(transgressor vs. control 1) and (victim vs. control 2)] identified regions that were commonly activated by both conditions, transgressor attended and victim attended.

Subsequently, contrast estimates of peak voxels in clusters of regions of a priori interest were extracted and correlated with personality measures (trait empathy (BEES), anxiety and anger expression) to examine whether individual differences in trait affect account for variability in brain activation. In addition a whole brain correlational analysis between BEES scores, as the personality measure with the strongest a priori hypothesis, and the response to transgressors versus victims was computed. Regions were evaluated using a statistical threshold of $p<0.001$ uncorrected for multiple comparisons and a cluster threshold of 15 voxels. No cluster threshold was applied to the amygdala due to this region's small size. Regions of a priori interest comprised the insula, the ventromedial and orbitofrontal cortex, temporal poles and the inferior lateral prefrontal cortex.

Results

Behavioral Results

Negative images and their respective controls reliably elicited the pre-selected target emotions (see Figure 3). Control persons for transgressors (control person 1) alike to their targets were almost exclusively males whereas the controls for victims (control person 2) were frequently females and children. We proceeded to examine whether these different characteristics of controls affected a participant's affective ratings. Paired t-tests revealed that participants felt neutral more often and happy less often towards control person 1 compared to control person 2, (t(20)=3.19, p<0.005 and t(20)=-3.86, p=0.001 respectively).

In addition to the emotion category, post-scan ratings outside the scanner also recorded the intensity of the experienced emotion (see Figure 4). From scan to post-scan, participants shifted on average 12.5% of their emotion category ratings. 5.2% (Range: 0 - 11.7%) of these shifts in ratings were shifts from feelings of fear to feelings of sadness towards victims, indicating a general difficulty of several participants to distinguish these two. Eleven participants never indicated feeling fear in response to transgressors and two never rated feeling fear with victims during the post-scan ratings. Due to the paucity and ambiguity of fear ratings, fear ratings were not included in the analysis of intensity ratings. Intensity ratings of anger towards transgressors and sadness to victims were contrasted directly and compared with happiness ratings of the controls by paired t-tests uncorrected for multiple comparisons. The intensity of experienced anger to transgressors did not differ significantly from that of sadness ratings to victims (t(20)=0.77, p>0.44). Sadness and anger were both of higher intensity than happiness to either control person (all ps<0.001). The intensity of happiness ratings to control person 1 did not differ significantly from control person 2 (t(20)=-1.23, p>0.23).

A strong correlation between intensity ratings of anger towards transgressors and sadness towards victims was observed (r=0.77, p<0.001). A positive correlation was also observed between happiness ratings to control person 1 and control person 2 (r=0.88, p<0.001).

Personality Measures

For descriptive statistics of personality measures see Table 8.

As explained previously (see Methods: Personality Measures), only trait empathy (BEES-Scale), trait anxiety, anger and anger expression (AX-Index) were entered into correlational analyses. Given the small sample size the correlation between trait anger and anxiety did not reach significance (r=0.22, p>0.3). Trait anger correlated positively with anger expression (r=0.45, p<0.05) and trait empathy (BEES, r=0.45, p<0.05). One should be cautious in interpreting the correlation between BEES scores and trait anger as removing one participant with high scores in both of these measures from the analysis reduced this correlation below significance ($r=0.27$, $p>0.2$).

Personality Measures and Subjective Emotion Ratings

Strong positive correlations between trait empathy (BEES scores) and intensity ratings of experienced sadness to victims ($r=0.56$, $p<0.01$) as well as anger towards transgressors were observed ($r=0.61$, $p<0.01$). No significant correlations between other emotional traits and intensity ratings of target emotion categories were observed.

Results fMRI

Results 5 sec Model

Regions that were commonly activated by transgressors and victims relative to the respective controls were revealed using a conjunction analysis ([transgressor vs. control 1] and [victim vs. control 2]). Significant activation differences are displayed in Figure 5 and Table 9. Activation differences were observed in bilateral occipital cortices extending into ventral temporal as well as posterior parietal regions. In addition, bilateral lateral prefrontal activations were found. These were of larger spatial extent in the left hemisphere extending from the anterior dorsal insula, over inferior and middle frontal gyri up to supplementary motor regions. Further activation differences were observed in the basal ganglia and in the thalamus.

Our primary interest was to identify regions that were differentially activated towards transgressors relative to victims. Results for the comparison of transgressors versus victims attended and vice versa are displayed in Table 10. A significant stronger response to transgressors relative to victims emerged in the right ventromedial prefrontal cortex, the right insula, bilateral middle temporal gyrus and the left superior temporal sulcus. In the reverse contrast, a stronger response to victims relative to transgressors emerged in the left inferior frontal gyrus and in the right caudate nucleus.

In order to assure that these differential patterns of brain activity were not simply due to observable differences in the age or gender of transgressors and victims, activation when participants attend to matched controls for transgressors (control 1) was contrasted with activation for the matched controls for victims (control 2). Activity in none of the above mentioned areas of interest significantly differed when control person 1 or control person 2 were attended (see Table 10). The right paracentral lobule was differentially more activated to control person 1 vs. control person 2. No significant activation differences were observed in the reverse contrast. To further ensure that activation differences between transgressors and victims were not driven by differential person characteristics (e.g. males versus females) or by attending towards different persons in a scene, interaction contrasts were computed.

The interaction contrast of ([transgressor vs. control 1] vs. [victim vs. control 2]) and the reverse interaction yielded similar patterns of activation differences as the simple contrasts of transgressors vs. victims and the reverse contrast respectively. Because of the lower statistical power of interaction contrasts, activation differences in some regions did not reach significance at $p<0.001$. Since, apart from this, activations in interaction contrasts and simple contrasts were similar, only the results for direct comparisons of transgressors vs. victims are reported.

Results Onset Model

In addition to the statistical analysis of primary interest which modeled each picture with a boxcar length of 5 seconds starting at the onset of each picture, a second model was computed with a standard hemodynamic response function at the onset of each image (onset model). This model aimed to capture activation differences in regions that are transiently activated. Table 11 displays results for simple contrasts of transgressors vs. victims and vice versa. As hypothesized, contrasting transgressors with victims yielded a significant activation difference in the left dorsal amygdala (*xyz*=[-22,-2,-12], Z=3.32, 8 voxels). Further regions that were differentially more activated to transgressors relative to victims comprised the left circular insular culcus, the left middle temporal gyrus, bilateral superior temporal gyrus, the left lingual gyrus and bilateral cuneus. The reverse comparison of victims versus transgressors yielded differential activity in the left superior precentral sulcus.

Correlational Analysis

To investigate whether trait empathy, as the personality measure with the strongest a priori hypothesis, was significantly correlated with brain activation to transgressors relative to victims, a whole brain correlational analysis was computed between the contrast of transgressors versus victims and trait empathy scores (BEES Scores). Clusters in which BEES scores correlated significantly with activation differences in both models (5 sec model, onset model) are listed in Table 12. In the 5 second model, contrast estimates for transgressors versus victims correlated negatively with BEES scores in the right ventral insula, the subgenual anterior cingulate cortex and in the left parieto-occipital fissure. No significant positive correlations between contrast estimates and BEES scores in any gray matter regions were observed. In the onset model, a positive correlation between contrast estimates to transgressors versus victims and BEES scores was present in the right and left amygdala, the left precuneus and the inferior parietal gyrus. Conversely, a negative correlation emerged in the left precentral gyrus and a cluster in the right superior temporal gyurs.

Trait Empathy and the Amygdala Response (image onset model)

The whole brain correlational analysis for BEES scores in the onset model yielded a significant positive correlation in the right amygdala (*xyz*=[28,-8,-20], Z=5.26, 102 voxels) and left amygdala (*xyz*=[-28,-10,-24], Z=3.72, 5 voxels). As depicted in the scatterplots (see Figure 6 b, c) individuals high in trait empathy had positive contrast estimates whereas individuals low in trait empathy had negative contrast estimates that increased towards positive values in individuals with moderately low empathy scores. This pattern suggested the presence of an interaction between high and low empathy subgroups and the amygdala response to transgressors versus victims. To explore this relationship further, we performed a median split resulting in two subgroups, 11 low empathic individuals and 10 high empathic individuals. Subsequently, the activity while attending towards transgressors and victims was compared for each subgroup (see Figure 6 d). These analyses revealed that high empathic individuals responded significantly more to transgressors compared to victims, (right amygdala $t(9)=4.17$, $p<0.005$; left amgydala $t(9)=4.50$, $p<0.005$). The low empathic subgroup did not respond significantly more to victims, (right amygdala $t(10)=-0.72$, $p>0.4$; left amygdala $t(10)=-1.04$, $p>0.3$) most likely due to the large inter subject variability of the amygdala response within this subgroup (see Figure 6 d).

Subsequent analyses investigated whether the correlation in the right amygdala was specific to empathy, or instead reflected a coarse threat sensitivity to transgressors relative to victims that was equally present in individuals high in trait anxiety, anger or anger expression. In order to do so, contrast estimates of the peak voxel in the right amygdala, that is the voxel which yielded the strongest correlation with trait empathy (xyz=[28, -8, -20], Z=5.26), were extracted and correlated with the remaining three measures of trait affect. We observed a positive correlation for trait anxiety ($r=0.59$, $p=0.005$) as well as for trait anger ($r=0.45$, $p<0.05$). When entering BEES scores, trait anxiety and trait anger simultaneously in a regression model to predict the amygdala response, the parameter estimate for trait anger decreased below significance (beta=0.10, $p>.45$) and only trait empathy (beta=0.62, $p<0.001$) and trait anxiety (beta=0.40, $p=0.005$) remained significant predictors. A median split based on participants' trait anxiety scores indicated that individuals high in trait anxiety responded significantly more to transgressors compared to victims ($t(9)=4.27$, $p<0.005$), whereas individuals low in trait anxiety responded to neither target person significantly more ($t(10)=-0.59$, $p>0.5$). No correlation between the cluster in the left amygdala and trait anxiety emerged ($r=0.07$).

We proceeded to examine whether the positive relation between trait empathy and the amygdala response to transgressors versus victims also applied to the activation difference in the left dorsal amygdala which was observed in the contrast of transgressors versus victims in the onset model (for results of the simple main effect contrasts see Table 11). We observed a positive correlation between BEES scores and the amygdala response in the peak voxel of activation ($r=0.43$, $p=0.05$) as well as a trend for a positive correlation with trait anxiety ($r=0.39$, $p=0.08$).

Trait Empathy and the Subgenual Anterior Cingulate Response (5 sec model)

The whole brain correlational analysis yielded a significant negative correlation between BEES scores and the response to transgressors versus victims in the right subgenual anterior cingulate gyrus (subgenual ACC) (see Figure 7 b). To investigate this interaction

further, a median split was performed based on participants' BEES scores and the activity while attending towards transgressors and victims was compared for each subgroup (see Figure 7 c). Individuals low in trait empathy, responded significantly more to transgressors relative to victims, ($t(10)=4.16$, $p<0.005$), whereas individuals high in trait empathy responded significantly more to victims, ($t(9)=-2.80$, $p<0.05$).
Furthermore, a negative correlation between the subgenual ACC response and the right amygdala response to transgressors versus victims was observed; $r=-0.74$, $p<0.001$. When controlling for the variance accounted for by BEES-scores, this correlation remained a trend (beta=-0.385, $p=0.08$).

Trait Empathy and the Insula Response (5 sec model)

A significant negative correlation between BEES scores and the response to transgressors vs. victims was also observed in the right ventral insula (5 sec model, Figure 8). The scatterplot (see Figure 8 c) depicts that contrast estimates for individuals low in trait empathy were positive whereas contrast estimates for individuals high in trait empathy were close to zero or negative. To examine this relationship further, a median split was performed and activity to transgressors and victims was compared for each subgroup (see Figure 8 b). Individuals low in trait empathy responded significantly more to transgressors relative to victims, ($t(10)=3.59$, $p=0.005$), and a trend for a stronger response to victims was observed in individuals high in trait empathy, ($t(9)=-2.13$, $p=0.06$). A similar pattern was observed in the right superior middle insula, which yielded a significant activation difference in the main effect of transgressors versus victims (see Table 10). Individuals low in empathy responded significantly more to transgressors versus victims, ($t(10)=3.72$, $p<0.005$), whereas this difference did not reach significance for individuals high in trait empathy ($t(9)=2.01$, $p=0.08$).

Correlational Analysis - Regions of a priori Interest

We proceeded to examine whether activation differences observed in simple contrasts of transgressors versus victims or vice versa were significantly correlated with measures of trait affect (BEES scores, trait anger, anxiety and anger expression). In order to do so, parameter estimates for the peak voxel in regions of a priori interest (vmPFC, left inferior prefrontal cortex) were extracted and interrelated with measures of trait affect.

In the ventromedial prefrontal cortex, it was found that the stronger response to transgressors relative to victims (see Table 10, Figure 9) was positively correlated with anger expression (see Figure 9 c). Confirming that this relation was specific to anger expression and not a concomitant effect of individual differences in trait empathy, partial correlations that isolated the effect of each trait on the vmPFC response yielded a significant positive correlation for anger expression (beta=0.55, $p<0.05$), but not for trait empathy (beta=-0.22,$p>0.28$).

No further correlations between measures of trait affect and activation differences between transgressors and victims in any regions of a priori interest (left inferior prefrontal cortex) were observed.

Discussion

The goal of the present study was to investigate neural correlates of stimulus evoked anger and empathic concern (sadness) using emotionally evocative social pictures. In order to identify transient activations related to the initial processing of the respective target person as well as brain processes that sustain throughout the whole image presentation, two statistical models were computed: an image onset model which captured initial activation differences between the respective conditions and a 5 sec model which delineated activations that pertained throughout the image presentation. Consistent with our hypothesis, focusing a participant's attention on transgressors or victims of a scene elicited feelings of anger and sadness respectively. These two emotions were associated with differential activity in brain regions implicated in affective processing. In particular, focusing a participant's attention toward the transgressor relative to the victim triggered a transient (onset model) response in the amygdala followed by more sustained (5 sec model) insular and ventromedial prefrontal activations associated with subjective states of anger towards the harm-doer. In addition, these patterns of neural activity were modulated by individual differences in trait empathy and anger expression. Conversely, sadness towards suffering victims relative to anger was associated with increased activation in the left inferior frontal gyrus (5 sec model), a region implicated in sympathy towards sad individuals (Decety & Chaminade, 2003). The differential activations in the amygdala, ventromedial prefrontal regions and insula as well as their modulation by individual differences in trait affect are discussed in detail below.

The Amygdala

As expected, we observed a significantly stronger response of the amygdala to transgressors, the source of threat towards the well being of a human fellow, relative to victims. Of importance to highlight, the differential amygdala response to transgressors relative to victims was only observed in the image onset model and not in the 5 sec model, indicating that it was transient and reflected the initial affective reaction towards the respective target person. This is consistent with models that highlight the amygdala as a key region in the processing and detection of threatening or salient information in our surroundings (LeDoux, 2000). Interestingly, the differential response to transgressors versus victims was modulated by an individual's levels of trait empathy. Specifically, whereas individuals high in trait empathy showed greater amygdala activation to transgressors versus victims, this differential response was not observed in individuals low in trait empathy. Once more, these correlations only emerged in the image onset model and not in the 5 sec model. The same modulation of the amygdala response also applied to individual differences in trait anxiety, in particular for the right amygdala. This is consistent with theoretical models and empirical evidence suggesting an enhanced sensitivity of anxious individuals towards threatening information as well as a stronger amygdala response towards cues of threat (Bishop, 2008; Bishop et al., 2004; MacLeod & McLaughlin, 1995; Mogg & Bradley, 1998).

Previous fMRI studies that investigated the influence of trait anxiety on the amygdala response to signals of threat under varying levels of attention usually employed more radical modulations of attention and stimuli that trigger an intrinsic and automatic threat response (e.g. fearful faces). This allowed the comparison of conditions in which threat cues were fully attended with conditions in which these intrinsic threat signals were likely outside of a participant's awareness. Employing such an attentional modulation, Bishop and colleagues (2004) observed that the amygdala in high state anxious individuals responded more strongly to fearful relative to neutral faces independent of whether or not participants attended towards these faces, suggesting a certain amount of automaticity of the amygdala response. In contrast, low anxious individuals showed a stronger amygdala response towards attended fearful faces only, suggesting that the sensitivity to threat outside the focus of spatial attention may be specific to high anxious individuals. In the present paradigm, the attentional modulation was more subtle and did not aim to prevent participants from perceiving the transgressor in the periphery. Rather, participants were encouraged to perceive the scene prior to engaging towards the respective target person. Unlike previously applied intrinsic threat signals, the complexity of the social scenes used here likely required a certain amount of active processing in order to identify the transgressor as the threat. Hence, present findings are not relevant to the debate of whether or not the amygdala response to threat may be pre-attentive or automatic. Instead, the results address the related issue of whether or not the amygdala response towards a consciously perceived elevated form of threat can be modulated by focusing a participant's attention either towards or away from this threat. Indeed, the present results indicated that this is the case. Focusing the attention and emotional engagement of anxious and empathetic individuals away from a perceived source of threat (the transgressor) and towards the victim modulated the amygdala response, yielding significant activation differences between these two conditions. Low trait anxious individuals in contrast were not sensitive to the differential threat conveyed by the two target people.

Importantly, the stronger amygdala response to transgressors in high empathetic individuals was not merely an effect of concomitant high levels of trait anxiety, as both traits significantly predicted the amygdala response when entered simultaneously in a regression model. The current results therefore suggest that the increased amygdala response of high empathic individuals to transgressors derives from their concern for and shared feelings with victims. High empathic individuals may feel more with the victims, and as a consequence, respond more strongly towards the source of threat to the individual. This was reflected in an increased amygdala response. Thus, the initial response to threat, as a trigger for anger or fear, was stronger for high empathic individuals.

The Ventromedial Prefrontal Cortex

Consistent with previous findings which ascribed the vmPFC an important role in the regulation of impulsive aggressive behaviors as well as in angry mood states (Blair, 2004; Coccaro et al., 2007; Dougherty et al., 2004), we observed a differentially stronger response to transgressors versus victims in this region. The differential vmPFC response emerged in the 5 sec model suggesting that it pertained throughout the image presentation reflecting the active emotional engagement towards the respective target person. This indicates that the vmPFC does not respond uniformly across negative emotional states, but that distinct negative emotions activate this region differentially.

It is necessary to mention that the increased vmPFC response to transgressors versus victims occurred via a modulation of activation decreases relative to controls. More specifically, activation decreases to transgressors were more attenuated than to victims yielding an overall stronger response to transgressors in the direct comparison of these two conditions. The vmPFC belongs to a network of brain regions with a high "resting state" activity (Fransson, 2005; Gusnard et al., 2001; Pitroda et al., 2008; Raichle & Gusnard, 2005). Given its high resting state activity, significant activation changes in this region likely implement a regulatory switch to control activity in other cortical or subcortical structures. In particular, activation decreases to negative or arousing emotional stimuli are a commonly reported phenomenon in the literature (Northoff et al., 2007; Simpson et al., 2000). The present findings show that activation decreases to transgressors are less pronounced then decreases to victims suggesting a differential recruitment of this region in anger versus empathic concern or sadness.

Evidence from lesion studies as well as imaging research implicates the vmPFC in the experience of moral emotions and in the regulation of social affective responses (Beer et al., 2003; Damasio et al., 1990; Harenski & Hamann, 2006; Moll et al., 2002). More specifically, it is hypothesized that the vmPFC integrates affective information from the amygdala to trigger a suitable behavioral response such as withdrawal or approach behaviors to the respective stimulus (Blair, 2007). One of the most distinguishing characteristics between different emotions is their tendency to elicit and motivate different behaviors. Whereas anger motivates punishment and aggression, sympathy and compassion motivate helping and consolidation behaviors (Eisenberg, 2000; Frijda, 1986;

Hoffman, 1990). Given the proposed role of the vmPFC in regulating behavioral responses, the activation differences observed may thus represent the distinct behavioral motivations elicited by transgressors relative to victims. This does not necessitate that participants consciously experienced a strong urge or impulsive to act against the harm-doer, but merely that the body's state and motor preparedness was attuned towards the behavioral motivations evoked by the respective target person.

In addition to regulating behavioral or affective responses, the vmPFC exerts an important role in guiding choice behavior among options that convey similar and thus competing expected values (Kringelbach, 2005). More specifically, the vmPFC has been suggested to convey a modality independent "common currency" by integrating the value of distinct stimuli and goals into a common code (Kable & Glimcher, 2007; Plassmann et al., 2007). Recent findings suggest that this common currency may also comprise the affective valuation of fellow human beings, which is consistent with a general implication of this region in social or moral emotions (Young & Koenigs, 2007). For instance, Singer and colleagues (2004a) observed that activation in the vmPFC is modulated by the acquired affective value of fellow human beings. More specifically, perceiving faces of players who had played unfairly in a social game, the Prisoner's Dilemma, increased activity in the vmPFC differentially more compared to faces of neutral affective status. Based on this evidence, one may suggest that the activation differences observed in the vmPFC in the current study, next to behavioral regulation, may also represent the distinct affective valuations of transgressors as the wrong doers versus victims as the maltreated recipients. Interestingly, the enhanced vmPFC response to transgressors was predicted by high levels of anger expression suggesting that individuals who tend to express their angry feelings might differentiate more strongly in their affective valuations between transgressors and victims as well as in their behavioral motivation towards these individuals.

The differential response to transgressors and victims in the vmPFC was predicted by individual differences in anger expression and not by individual differences in trait empathy. In this region, the correlation coefficient of the relation between trait empathy and the vmPFC response was negative, albeit non significant. For trait empathy, a significant negative correlation emerged in an adjacent ventromedial region, the subgenual anterior cingulate gyrus.

The Subgenual Anterior Cingulate Gyrus

In the 5 sec model, a significant negative correlation between trait empathy and the differential activity to transgressors versus victims was observed in the subgenual anterior cingulate gyrus. Specifically, individuals low in trait empathy showed a larger deactivation in this region towards victims relative to transgressors resulting in an overall stronger response to transgressors. In contrast, high empathic individuals deactivated this region more strongly for transgressors relative to victims, yielding a stronger response to victims in the direct comparison of these two conditions.

As noted above, deactivations in vmPFC regions are commonly observed in fMRI studies. Simpson and colleages (2000) proposed that ventromedial deactivations are not of specific emotional nature but are shaped by cognitive as well as affective processes. For instance, evidence implies larger vmPFC activation decreases under increasing attentional demands given low affective contribution (e.g. low performance anxiety) (Simpson et al., 2001a; Simpson et al., 2000; Simpson et al., 2001b). Tasks that are more demanding require more system resources and hence yield larger deactivations in this region (Shulman et al., 1997; Simpson et al., 2001b). Thus, a possible interpretation of the interaction between trait empathy and the subgenual anterior cingulate response is that it reflects attentional preferences between subgroups. Specifically, for highly empathic individuals, it may follow intuitively and naturally to attend towards and empathize with the distressed victim. In turn, detaching from victims and allocating their feelings and attention towards transgressors may require more system resources yielding a stronger deactivation towards transgressors relative to victims in the subgenual anterior cingulate cortex (subgenual ACC). Individuals low in trait empathy may find it easier to attend towards transgressors and project anger upon these harm-doers than nurturing empathic concern for victims. This is supported by a decrease in subgenual ACC activation towards victims relative to transgressors.

Why would one suspect low empathic individuals to attend more easily towards transgressors? In the present paradigm, anger was the only emotion that did not necessitate shared feelings or empathy with any target person in a scene. To illustrate this point, we may feel anger at someone who laughs while making a racist comment. In this case our feeling of anger towards this person differs markedly from the emotion experienced by this person. Consequently, anger may be experienced in two distinct forms in the present study: One may feel anger towards a transgressor as a direct self derived emotional state against a person who acts counter to shared social norms and values, or alternatively one may experience empathic anger towards a transgressor which derives from shared feelings and concern for the victim's distress. Low empathic individuals, in general may not respond strongly to the present stimuli, as is also indicated by their undifferentiated amygdala response towards transgressors versus victims. However, out of all conditions, they might experience more success in engaging towards transgressors and experiencing this direct self derived form of anger. This interpretation is supported by the activation pattern observed in the insula.

Insula

Present findings of the 5 sec model indicate that anger and sadness are associated with significant activation differences in the right insula, in particular middle and ventral insular regions. This is consistent with accounts ascribing this region an important role in the general experience of social emotions (Singer, 2007). Based on its connections to regions implicated in the processing of sensory information, pain perception and general viscerosensation, the insula has been ascribed a key role in integrating bodily states that accompany either one's own direct affective experience or affective experiences that arise from empathizing with other individuals (Craig, 2002, 2003; Singer & Frith, 2005). These integrative processes are thought to create a sense of emotional self awareness that is crucial for the subjective experience of emotional states (Craig, 2002; Damasio, 1999; Damasio et al., 2000).

In the present study, the insula response was stronger to transgressors relative to victims, in particular in the mid insula. This is consistent with findings of (Zahn et al., 2008), which implicate insula involvement when experiencing anger or indignation towards another person. Furthermore, this anger related activation was modulated by individual differences in trait empathy. Individuals low in trait empathy responded differentially stronger to transgressors relative to victims. This clear cut differential insula response towards either target person was not observed in high empathic individuals. In particular, individuals high in trait empathy showed a trend towards a stronger response in the ventral insula to victims relative to transgressors. This is consistent with the activation pattern observed in the subgenual cingulate anterior gyurs which suggested that low empathic individuals may attend preferentially to transgressors, while high empathic individuals attend preferentially towards victims. Moreover, the fact that a similar pattern also emerged in the insula supports the notion that low empathic individuals more readily experience a subjective feeling state of anger to transgressors relative to sadness for victims.

The low empathic peer: No empathy but some anger ?

Interestingly, the decreased subgenual ACC response to transgressors in high empathic individuals opposes the activation pattern revealed by this subgroup in the amygdala, where high empathy was associated with a differentially stronger response to transgressors relative to victims. One possible explanation is that the initial amygdala response to transgressors in high empathic individuals reflects a transient reaction towards the threat imposed upon the victim yielding a coarse feeling of negative arousal. In turn, maintaining attention onto the transgressor and engaging in anger towards this person appears more effortful for low empathic individuals, as suggested by the activation patterns in the subgenual ACC and insula. In contrast, low empathic individuals may not respond strongly to the threat imposed upon the victim nor be overly pre-occupied with the victim's distress. The differentially larger deactivation to victims relative to transgressors in the subgenual ACC jointly with the consistently stronger insula response to transgressors versus victims suggests that these individuals succeed in experiencing a subjective feeling state of anger. Importantly, this anger response may not necessarily be more intense as that experienced by high empathic peers but instead merely reflect a distinct subjective feeling state of anger; namely a self derived experience of anger towards a harm-doer acting against one's own values rather than an anger experience on behalf of a victim's distress (empathic anger). The notion that the insula activation observed in the present study may reflect this self derived feeling of anger is also implied by Zahn and colleagues (2008), who found this region activated when participants imagined scenarios of another person acting counter their own values.

Behavioral Ratings: A Contradiction ?

Trait empathy did not only correlate positively with intensity ratings of experienced sadness towards victims but also with the intensity ratings of anger towards transgressors. However, the behavioral findings do not necessarily contradict the above interpretation that experiencing anger towards transgressors may have been more effortful for high empathic individuals. For instance, the increased amygdala response towards transgressors may have reflected a coarse state of negative arousal and fear on behalf of the victim. It may have been differentially more effortful for these individuals to maintain their attention upon the transgressor and translate this arousal into anger, compared to engaging towards the distressed victim. This may well yield similar intensity ratings despite underlying differential efforts to experience the two emotions. Furthermore, instead of capturing the intensity specific to anger and sadness, the behavioral ratings may have picked up a general arousal response towards the scene that preceded the more differentiated subjective feeling states of anger and sadness. This is supported by the strong positive correlation between intensity ratings of sadness and anger. The strength of this correlation suggests that both emotion ratings towards either target person reflected the same underlying construct, namely an overall arousal response towards the scene rather than the distinct subjective feeling states towards target persons. This arousal response may have been less present in low empathic peers.

The idea that dispositional empathic concern may be related to feelings of sadness for victims rather than anger towards their transgressors is supported in behavioral findings of (Vitaglione & Barnett, 2003). These investigators reported a positive relation between dispositional empathic concern and feelings of sadness towards a victim of drunk driving. However, empathic concern did not significantly predict levels of state anger. Furthermore, dispositional empathic concern positively correlated with an individual's desire to help the victim, but negatively predicted punishing desires towards the transgressor (Vitaglione & Barnett, 2003). This is consistent with the victim centered focus of attention of high empathetic individuals suggested by the subgenual ACC activation pattern in the present study. Hence, the present task might have forced highly empathetic individuals to resist their dispositional tendency to attend to and feel with the victim by demanding them to maintain attention upon the transgressor and turn a coarse threat response towards this harm-doer into anger.

Is it a Matter of Arousal?

One might propose that the differential brain activations towards transgressors and victims may be explained by arousal differences between anger and sadness; that is, by differential autonomic activations specific to each emotion. Indeed anger has been described as a high arousal emotional state whereas sadness is generally referred to as a low arousal emotion (Izard, 1993). It might be of interest for future research to measure skin conductance throughout scanning to delineate whether arousal differences between these two affective states explained variance in brain activation. However and important to emphasize this will not serve to answer any "either or" questions about whether autonomic differences or different subjective emotional experiences drove effects. Starting with early theories of emotion one has believed that different emotions should come along with different and specific patterns of autonomic activity (James, 1884). Henceforth arguments of whether or not differences of autonomic activity or rather differences in the subjective experience of anger and sadness drive distinct patterns of brain activations may be superfluous as both are believed to be interdependent and not dissociable. Given this approach, the only question that measures of autonomic activity in imaging studies will answer is whether or not autonomic patterns of activity as inherent characteristics of these distinct emotions explain variance in brain activation. Furthermore, despite strong theoretical claims and wide reaching efforts to delineate distinct emotion specific patterns of autonomic activity, to date research has not shown much success in reliably differentiating basic emotions based on their autonomic profiles (Cacioppo et al., 2000)

Future Directions and Limitations

The present findings have general implications for imaging studies that employ social emotional scenes, such as the IAPS. The results highlight that attending to different individuals in a scene elicits distinct emotions that are associated with differential patterns of brain activity in affect related regions. Furthermore, our findings suggest that individuals with different levels of trait affect might focus on different people within a scene, resulting in differential emotional experiences and hence differential brain activity. This effect generates variability between participants and, thus, might explain differential activation patterns across studies that used the IAPS, an image set with scenes well known to elicit various emotional reactions (Britton et al., 2006). It is therefore important to monitor the gaze of a participant when studying emotional reactions towards more complex social scenes and to measure individual differences of trait affect as potential modulators of these fixation patterns.

One limitation is that the present study did not employ eye tracking to verify that participants maintained visual attention towards the respective target person and thus engaged in the task. However, the emotion ratings that followed each picture confirm that the people in each scene consistently elicited the respective target emotions, suggesting that participants performed the task properly. Nevertheless, capturing fixation patterns of participants in these scenes without explicit task instructions will be of interest for future research in order to investigate whether the victim oriented attentional preference suggested by present findings indeed applies to high empathic individuals.

Another limitation of the present study is the fact that the sample consisted only of females. The literature highlights sex as a strong moderator of brain activations as well as behavioral responses related to the processing of emotional information (Cahill, 2006; Dickie & Armony, 2008; Hamann, 2005). Of particular importance to the present study, women have a stronger disposition to empathize with individuals in their surroundings than do males, and sex specific patterns of brain activation changes have been reported in empathy related paradigms (Mehrabian, 2000; Singer et al., 2006). Our conclusions are thus constrained to the female population and future studies are necessary to delineate whether these results apply to males. Our decision to test only females was due to the set of images applied. Despite attempts to equalize the present image set the vast majority of scenes displayed males as transgressors and females as victims. Therefore, males might have felt discriminated against because the images generalized their sex into violators and offenders of the victimized female. Such a defensive position might have prevented males from engaging in the picture and we therefore decided to constrain the present study to female participants.

One may object that the more intense negative emotional states elicited by scenes of interpersonal transgressions elicit longer lasting states of anger and sadness that may pertain into subsequent stimuli and thus potentially confound the emotional reaction to the latter. Indeed, this is a general problem and concern in event related designs that probe affective processes. Yet, several measures implemented in the present experimental design as well as evidence of previous research render it unlikely that the more intense affective states triggered by negative images did systematically alter the present findings. The time scope of specific elicited emotions (anger vs. happiness) during viewing of complex pictures remains to our knowledge unknown as little research has investigated emotion specific reactions towards complex scenes. However evidence supports that affective states evoked by static affective pictures or faces are weak rendering it improbable that they exceed the time of stimulus duration by more than several seconds (W. J. Davis et al., 1995; Wild et al., 2001). Since the precise duration of the evoked affective state is difficult to determine empirically, the present research alike to previous fMRI studies that employed event related designs displayed the set of affective pictures in a pseudo randomized manner in order to avoid any long lasting mood states as well as systematic carry over effects between emotion categories. Henceforth, it is unlikely that long lasting negative affective states had a profound impact on the present findings. On the other hand, this design probably resulted in the induction of low intensity transient emotions which may engage different brain areas and/or different levels of activation than more "ecological" or everyday angry or sad feelings.

The present study did not control for variations in hormonal levels as a potential confounding variable. Previous research has shown that variations in hormonal levels affect brain activity and more specifically individuals' BOLD responses during affective regulation to negative emotional pictures, which is of particular relevance to the present study (Tessner et al., 2006; Urry et al., 2006). For future studies, it is therefore recommended to assess variations in hormonal levels by means of blood or saliva samples to include these measures as covariates in the analysis.

Throughout development and testing of the present paradigm, we were not aware that meanwhile a measure of trait empathic anger had been developed and validated (Vitaglione & Barnett, 2003). These researchers have proposed a dissociation between measures of empathic concern and empathic anger in predicting changes of emotional states towards victims and transgressors. More precisely, dispositional empathic concern significantly predicted changes in sadness towards the victim, whereas empathic anger positively predicted state sadness as well as anger. The present results to some extent agree with these findings through the suggestion that individuals high in empathic concern engage their attention and feelings towards victims more easily. Furthermore, throughout behavioral pre-testing of the picture stimuli several participants reported engaging more easily towards victims and experiencing anger rather secondary, suggesting that in at least for a subset of our sample anger demanded more attention. It may be of interest to explore whether trait empathic anger covaries differently with activation patterns in the present sample as compared to empathic concern.

Summary and Conclusion

The present findings show that attending towards transgressors or victims of a scene elicits feelings of anger and sadness respectively which yield distinct patterns of brain activations in key regions of affective processing. More specifically, results imply that a set of limbic and paralimbic structures, the amygdala, insula and vmPFC, respond differentially to anger versus sadness/empathic concern. These activation differences are strongly modulated by an individual's levels of trait empathy. Such differential activation patterns of high and low empathic individuals indicate that they differ in their subjective emotional experience to transgressors versus victims.

The initial and transient stronger amygdala response of high empathic individuals to transgressors may be interpreted as a stronger response towards the threat on behalf of the victim. In particular, the differentially larger deactivation in the subgenual ACC towards transgressors suggests that high empathic individuals engage more easily in directing their feelings towards the victim. Consequently and also suggested by a trend towards a stronger response to victims in the ventral insula, their anger may derive from feelings of concern for victims as a prototypical type of "empathic anger". In contrast, in low empathic individuals the amygdala response was not stronger when viewing the transgressor as the source of threat towards the victim. Furthermore, the larger deactivation for victims relative to transgressors in the subgenual ACC suggests that this subgroup engages more easily towards the transgressor. In addition the consistently stronger insula response towards transgressors versus victims in low empathic individuals indicates that this attentional preference is also associated with a clearly differentiated subjective feeling state towards the transgressor relative to the victim. This suggests that in these individuals anger may be more self derived and directly projected towards a harm doer who acts against one's values, rather than taking a detour over feelings of concern for the victim.

At the conceptual, these data suggest that there might not be one single subjective experience and activation pattern of anger, but different sub-types, namely empathic and self derived anger. The vmPFC appears to play a more general role in the regulation and expression of angry feeling states, as suggested by a positive correlation with an individual's tendency to express anger and the vmPFC response to transgressors versus victims. Theories postulate anger to be a more cognitive emotion that involves appraisals of agency and unfairness (Clore & Centerbar, 2004). Hence the interplay between the amygdala response and vmPFC activation pattern might have reflected appraisal processes that shaped an initial state of arousal into an affective experience of anger.

General Conclusion

The projects of this thesis investigated the effects of anger on risk behavior as well as its neural correlates as a stimulus evoked affective state. Findings of these projects confirm that trait anger and anxiety influence an individual's levels of optimism in opposite directions. However, they do not yield support that these biases translate into behavioral differences in risk taking. Rather than cognitive biases such as likelihood perceptions they point towards impulsivity as a factor that may yield inconsiderate and thus at times risky behaviors in both, high trait anxious as well as angry individuals. In particular the tendency of individuals high in anger expression to engage in risk behaviors was mediated by impulsivity. Thus present findings suggest that factors such as impulse control and affective coping styles, rather than optimism, underlie the risk proneness of some angry characters.

Instead of investigating the effects of anger as an emotional trait on an individual's behavioral preferences, the second project focused on the subjective feeling state of anger. In particular it examined how anger differs from empathic concern (sadness) in its neural correlates. Present findings confirm the role ascribed to the vmPFC by previous research in the regulation and experience of angry feeling states. Furthermore they highlight individual differences in trait empathy as strong modulators of activity in affect related regions related to the engagement to transgressors versus victims. These distinct activation patterns suggest that high and low empathic individuals differed in their emotional reaction towards these scenes and thus likely in their subjective feeling state of anger and sadness. This implies that one may need to give up the notion that there is one type of anger experience with a specific underlying activation pattern, but instead adopt the view that distinct subtypes of anger may exist which are reflected by differential activation patterns in the insula and amygdala. Whereas a cognitive self derived form of anger relative to sadness may be more closely related to activation differences in the insula, empathic anger as a reaction towards a threat on behalf of another individual's distress appears to derive from initial activation differences in the amygdala. The vmPFC appears to play a more general role in the regulation of angry feelings.

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TABLES

Table 1: Descriptive statistics for self report measures and the BART.

Measure	Mean	SD	Range
Trait Anger	19.5	5.1	11 - 33
Anger Expression	33.33	11.00	8 - 59
Trait Anxiety	39.1	9.0	23 - 66
Neuroticism	21.6	8.5	1 - 42
Optimism (Total)	0.7	0.8	-0.9 - 2.6
Optimism (Neg)	1.0	1.0	-1.46 - 3.12
Optimism (Pos)	0.4	1.0	-1.5 - - 3.0
Impulsivity (BIS)	68.0	10.5	45 - 92
Impulsivity (N-TCI)	3.9	2.6	0 - 10
Risk Taking	2.8	0.4	1.8 - 3.7
BART Score	27.6	11.6	7.3 - 62.5
GABS	75.9	14.7	39 - 109

Table 2: Summary of multiple regression analysis for variables predicting participants' total optimism scores

	Total Optimism Score		
Variable	B	SE B	β
Trait Anger	0.02	0.01	0.16
Anxiety	-0.23	0.07	-0.31*
Impulsivity	-0.24	0.07	-0.32*

Note. $R^2 = 0.23$
* $p < 0.05$. ** $p < 0.01$ *** $p < 0.001$

Table 3: Summary of multiple regression analysis for impulsivity and event expectancy as predictors of risk taking behaviors

	Total Risk Taking Score (DOSPERT)		
Variable	B	SE B	β
Event Expectancy	0.10	0.03	0.28**
Impulsivity	0.21	0.04	0.49***

Note. $R^2 = 0.31$
* $p < 0.05$. ** $p < 0.01$ *** $p < 0.001$

Table 4: Summary of multiple regression analysis for variables predicting participants' risk taking behaviors

	Total Risk Taking Score (DOSPERT)		
Variable	B	SE B	β
Trait Anger	-0.01	0.01	-0.06
Anxiety	-0.00	0.04	-0.01
Impulsivity	0.21	0.04	0.50***

Note. $R^2 = 0.24$
* $p < 0.05$. ** $p < 0.01$ *** $p < 0.001$

Table 5: Summary of multiple regression analysis for anger expression and impulsivity as predictors of participants' risk taking behaviors

	Total Risk Taking Score (DOSPERT)		
Variable	B	SE B	β
Anger Expression	0.00	0.00	0.03
Impulsivity	0.20	0.04	0.47***

Note. $R^2 = 0.23$
* $p < 0.05$. ** $p < 0.01$ *** $p < 0.001$

Table 6: Bivariate correlations between personality measures and risk taking in the BART

	Impulsivity	DOSPERT	GABS	T-Anger	Anxiety	Anger-E	Optimism
BART Score	0.02	0.21*	0.27**	-0.10	-0.09	-0.12	0.08

Note. DOSPERT = total risk taking score of DOSPERT risk behavior scale; GABS = total score of Gambling Attitudes and Beliefs Scale; T-Anger = Trait Anger score; Anger-E = Anger Expression score; Optimism = total score of Weinstein's measure of optimism

* $p < 0.05$ ** $p < 0.01$

Table 7: Summary of multiple regression analysis for trait anger and anxiety as predictors of risk taking in the BART (BART Score).

	BART Score		
Variable	B	SE B	β
Anger	-0.19	0.24	-0.08
Anxiety	-0.73	1.22	-0.06

Note. $R^2 = 0.01$

* $p < 0.05$. ** $p < 0.01$ *** $p < 0.001$

Table 8: Descriptive statistics for personality measures applied in the fMRI study

Personality Measure	**Mean**	**SD**	**Range**
State Anxiety	29.91	5.65	21 - 41
Trait Anxiety	35.90	9.03	22 - 51
Trait Anger	17.10	3.21	10 - 24
Anger Expression (AX-Index)	28.24	8.62	11 - 44
Trait Aggression (Buss-Perry)	61.86	11.55	42 - 90
Trait Empathy (BEES)	53.71	23.49	4 -105
IRI - Perspective Taking	18.43	3.20	12 - 26
IRI - Empathetic Concern	20.86	4.21	12 - 28
IRI - Fantasy Scale	19.24	5.16	7 - 27
IRI - Personal Distress	10.81	5.09	2 - 18
Trait Arousability	13.57	15.73	-13 - 50

Table 9: Areas that were commonly activated by transgressors and victims relative to their respective controls. Conjunction analysis: (transgressors vs. control 1) and (victim vs. control 2)

Brain Region	L/R	BA	Size	Z-Score	x	y	z
Right Lateral Occipital / Parietal/ Ventral Temporal Cortex			9596				
Lingual Gyrus	R	18		5.78	28	-80	-8
Middle Occipital Gyrus	R	19		5.6	38	-86	14
Superior Parietal Gyrus	R	7		5.43	38	-44	70
Precuneus	R	7		4.46	32	-50	58
Fusiform Gyrus	R	37		4.28	44	-46	-18
Cerebellum	R			4.75	32	-56	-30
Left Lateral Occipital / Parietal / Ventral Temporal Cortex			8155				
Inferior Occipital Gyrus	L	19		5.67	-42	-72	-10
Middle Temporal Gyrus	L	37		5.43	-50	-64	6
Fusiform Gyrus	L	37		5.24	-44	-52	-18
Superior Parietal Gyrus	L	7		5.07	-26	-56	66
Inferior Parietal Gyrus	L	40		4.38	-64	-32	32
Cerebellum	L			3.84	-28	-56	-30
Left Inferior Frontal Gyrus / Insula / Precentral Gyrus			4177				
Inferior Frontal Gyrus	L	46		5.11	-54	34	6
Precentral Gyrus	L	6		4.84	-42	-4	46
Inferior Frontal Gyrus	L	9		4.29	-60	12	26
Insula	L	13		3.44	-38	12	-2
Superior Temporal Gyrus	L	22		3.64	-52	10	-6
Right Inferior Frontal Gyrus/ Precentral Gyrus							
Inferior Frontal Gyurus	R	46	342	4.27	58	34	8
Inferior Frontal Gyrus / Fronto Insular Cortex	R	13		3.27	44	32	2
Middle Frontal Gyrus	R	9	77	3.62	46	20	26
Middle Frontal Gyrus	R		221	4.92	34	-6	48
Precentral Gyrus	R			4.39	44	-2	46
Superior Frontal Gyrus	L/R	6	384	4.59	0	4	62
Cingulate Gyrus		24	41	3.69	-2	12	30
Caudate	L		519	4.33	-12	-2	14
Thalamus	L			3.95	-14	-16	6
Lentiform Nucleus	L			3.38	-12	-4	0
Caudate	R		243	4.16	14	-2	14
Thalamus	R			3.22	16	-10	6

Note. Coordinates of local maxima ($p < 0.001$ uncorrected) are listed according to the MNI coordinate system; Cluster threshold: 15 voxels for activations in regions of no a priori interest; L/R: left/right; BA: Brodman Areas; Size: # of voxels

Table 10: Activation differences for simple main effect contrasts of the 5 second model.

Brain Region	L/R	BA	Size	Z-Score	x	y	z
Control 1 > Control 2							
White Matter	R	-	135	4.44	30	18	26
Paracentral Lobule	R	5	86	3.88	2	-28	62
Transgressor > Victim							
Ventromedial Prefrontal Cortex	R	32/10	96	3.52	4	48	-12
Insula	R	13	24	3.42	44	8	6
Precentral Gyrus	L	4	63	3.57	-44	-8	46
	L	4	16	3.41	-38	-14	58
Transverse Temporal Gyrus	R	41	177	4.13	46	-28	8
Middle Temporal Gyrus	R	21	128	3.84	60	-26	-8
	L	21	16	3.27	-60	-18	-10
Superior Temporal Sulcus	L	41	77	4.05	-54	-32	10
Cuneus	L/R	17/18	2119	5.26	-16	-98	12
Putamen	L		46	3.7	-26	0	2
	L		15	3.59	-30	-16	0
Cerebellum	L		38	4.11	-22	-56	-32
Victim > Transgressor							
Inferior / Middle Frontal Gyrus	L	46	237	3.55	-44	40	6
Caudate	R		31	3.67	12	18	14
	L		3	3.16	-10	16	10

Note. Coordinates of local maxima ($p < 0.001$) uncorrected for multiple comparison) are listed according to the MNI coordinate system; Cluster threshold: 15 voxels for activations in regions of no a priori interest; L/R: left/right; BA: Brodman Areas; Size: # of voxels

Table 11: Significant activation differences in simple contrasts of transgressors versus victims and vice versa in the onset model.

Brain Region	L/R	BA	Size	Z-Score	x	y	z
Transgressor > Victim							
Circular Insular Sulcus	L	13	17	3.45	-48	-4	8
Amygdala	L	-	8	3.32	-22	-2	-12
Middle Temporal Gyrus	L	21	84	4.19	-62	-20	-12
Superior Temporal Gyrus	L	42	16	3.32	-64	-26	10
	R	21	35	3.65	58	-22	-10
Collateral Sulcus	L	20	16	3.62	-32	-16	-26
Lingual Gyrus	L	19	153	4.09	-22	-48	-14
Cuneus	L/R	17/18	1355	5.6	10	-92	22
Putamen	L		83	3.8	-22	-4	4
Cerebellum	R		47	3.36	24	-6-	-12
Victim > Transgressor							
Superior Precentral Sulcus	L	6	30	4.07	-34	4	40

Note. Coordinates of local maxima ($p < 0.001$ uncorrected) are listed according to the MNI coordinate system; Cluster threshold: 15 voxels for activations in regions of no a priori interest; L/R: left/right; BA: Brodman Areas; Size: # of voxels.

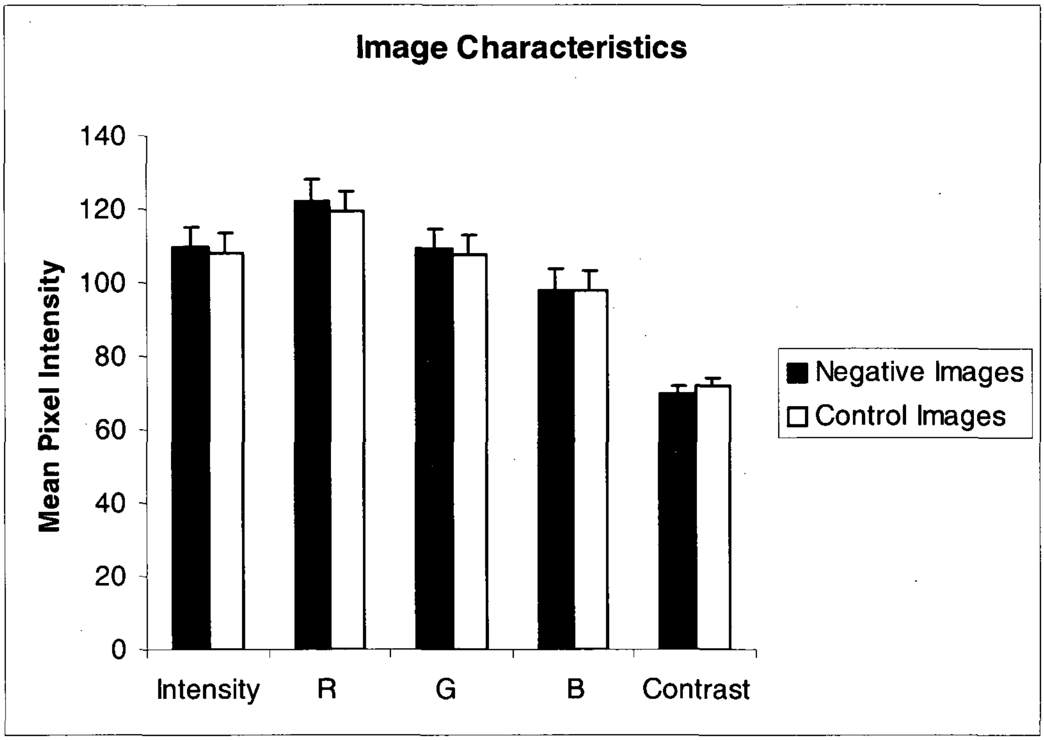
Table 12: Areas in which the response to transgressors versus victims correlated with trait empathy (BEES Scores) for the 5 second and the onset model respectively.

Brain Region	L/R	BA	Size	Z-Score	x	y	z
Positive correlation with trait empathy (5 second model)							
White Matter	L	-	27	3.57	-10	18	16
Negative correlation with trait empathy (5 second model)							
Ventral Insula	R	13	152	4.14	44	6	-12
Mid-Insula	R	13		3.34	42	0	2
Subgenual Anterior Cingulate	R	25	50	3.87	4	28	-2
Insular Sulcus	R		31	3.82	42	-14	-10
Parieto-Occipital Fissure	L	39	55	3.64	-4	-64	24
Positive correlation with trait empathy (onset model)							
Amygdala	R	-	102	5.26	28	-8	-20
Lateral Fissure	R		29	3.82	42	-42	30
Precuneus	L	31	15	3.79	-10	-44	40
Inferior Parietal Gyrus	L	40	17	3.34	-42	-40	46
Amygdala	L	-	5	3.72	-28	-10	-24
Negative correlation with trait empathy (onset model)							
Precentral Gyrus	L	4	84	3.81	-24	-16	56
Superior Temporal Gyrus	R	22	32	3.44	48	12	-14
Insula	R	13		3.26	48	4	-12

Note. Z-scores indicate the significance of the correlation between trait empathy (BEES Scores) and the BOLD contrast of Transgressors versus Victims. Coordinates of local maxima ($p < 0.001$ uncorrected) are listed according to the MNI coordinate system; Cluster threshold: 15 voxels for activations in regions of no a priori interest; L/R: left/right; BA: Brodman Areas; Size: # of voxels.

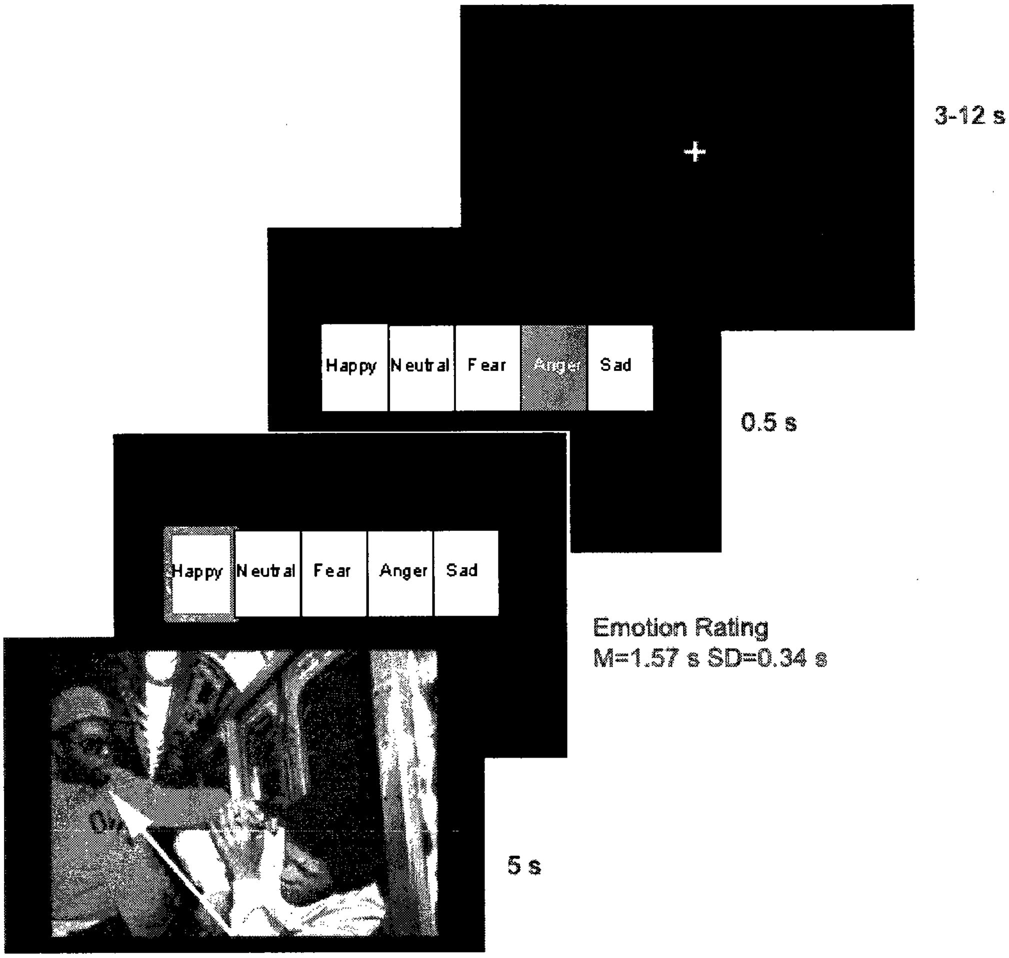
FIGURES

Figure 1



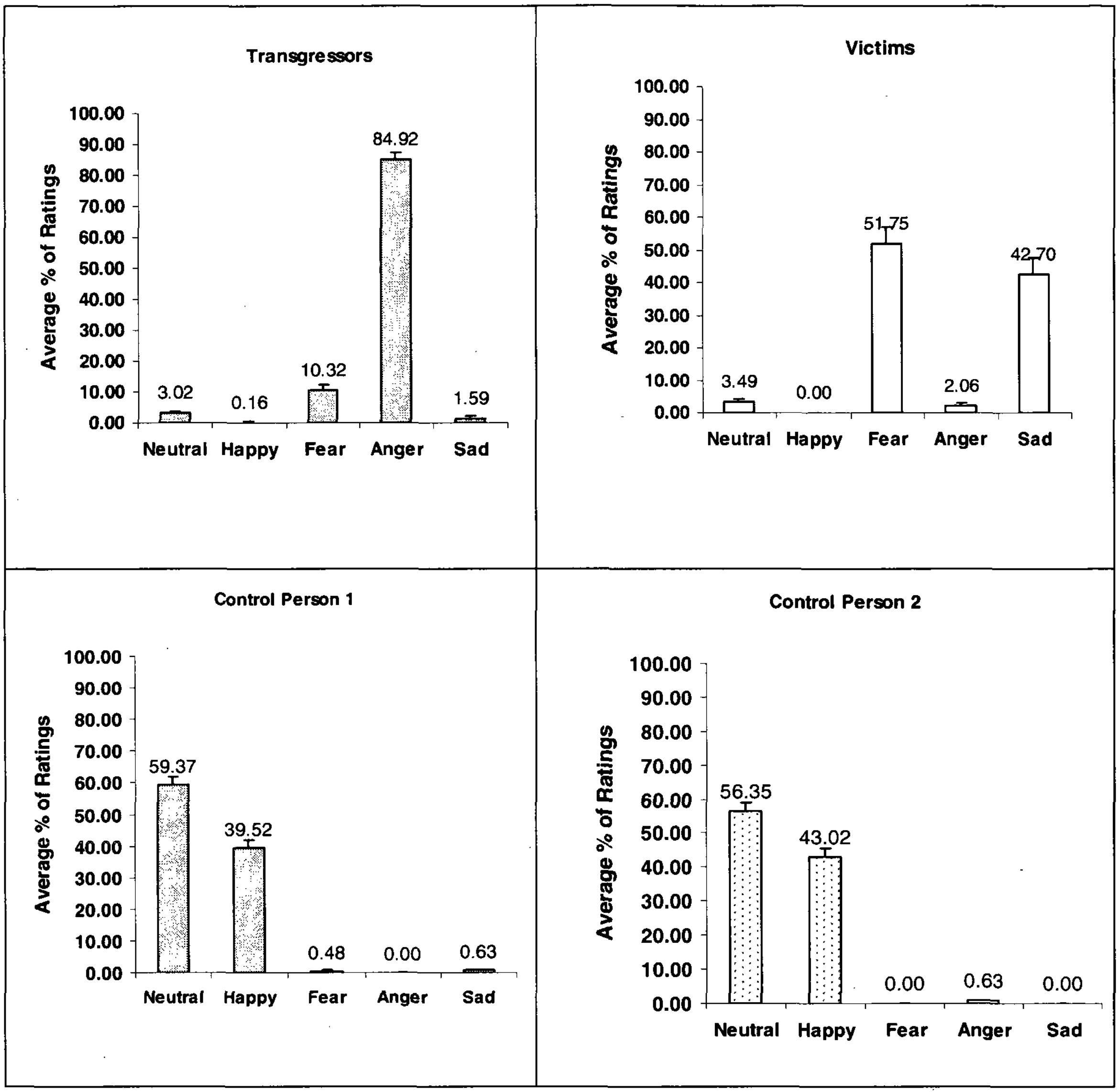
Displayed are the mean and standard error of the overall color intensity, red, green and blue intensities and contrast values for each image set (negative, control).

Figure 2



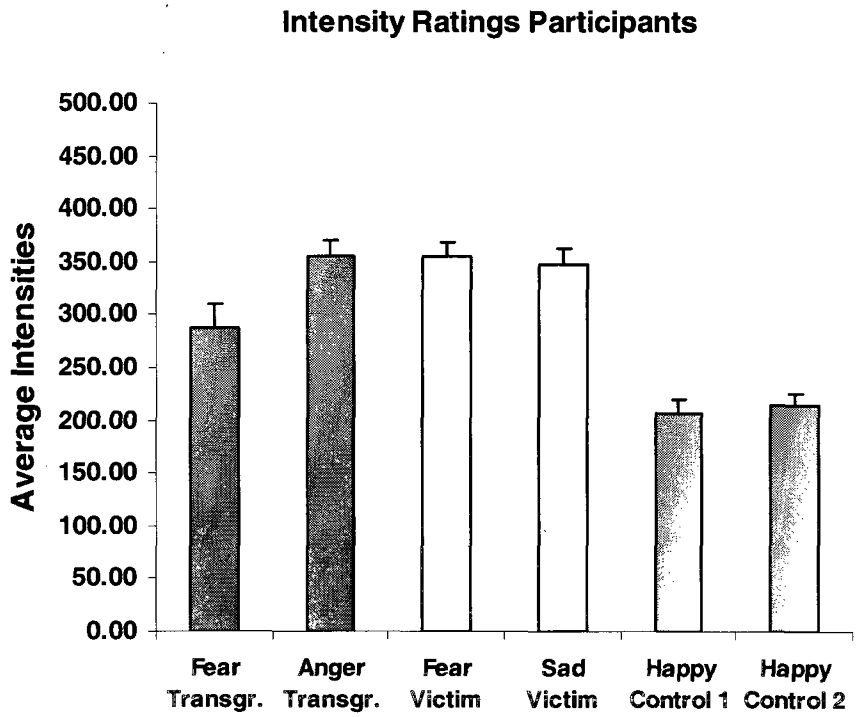
A representative trial from the fMRI session. Participants indicated the basic emotion felt towards the person demarcated by the arrow. The ITI varied between 3 and 12 seconds with a median ITI of 3 seconds. Duration of the emotion rating depended on the response times of participants, mean response time and standard deviation is displayed.

Figure 3



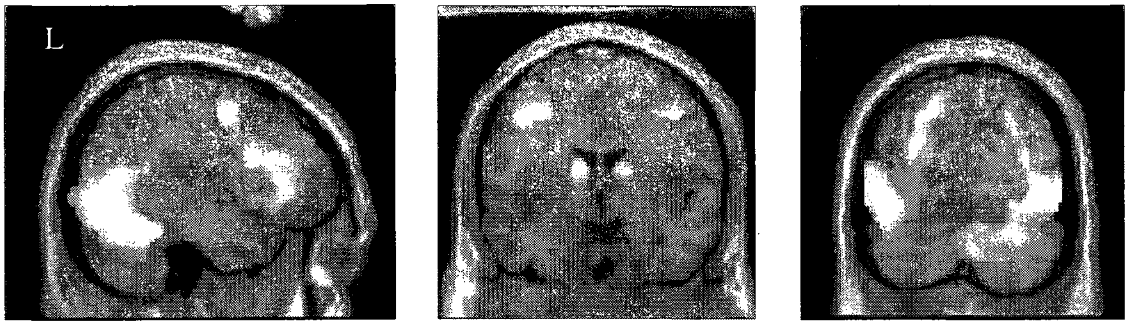
Basic emotion felt towards each target person category indicated by percentage of trails. Error bars represent the standard error of the mean.

Figure 4



Intensity ratings of participants for the respective target emotions. Error bars represent the standard error of the mean.

Figure 5



Common areas activated by transgressors and victims relative to their respective controls (conjunction analysis). Activation differences were found in bilateral lateral occipital cortices (BA18,19) extending into ventral temporal cortices (BA37) and posterior parietal regions (BA7,40). Bilateral lateral prefrontal activations extended from the insula, inferior frontal gyrus (BA47,46,45,44), middle frontal gyrus (BA9), into supplementary motor regions (BA6) to the precentral gyrus. These prefrontal activations were stronger and of larger spatial extent for the left hemisphere. In addition, significant activation differences were observed in the caudate nucleus (bilateral), thalamus (bilateral) and the left lentiform nucleus. Activations were evaluated at a threshold of $p < 0.001$ uncorrected for multiple comparisons.

Figure 6

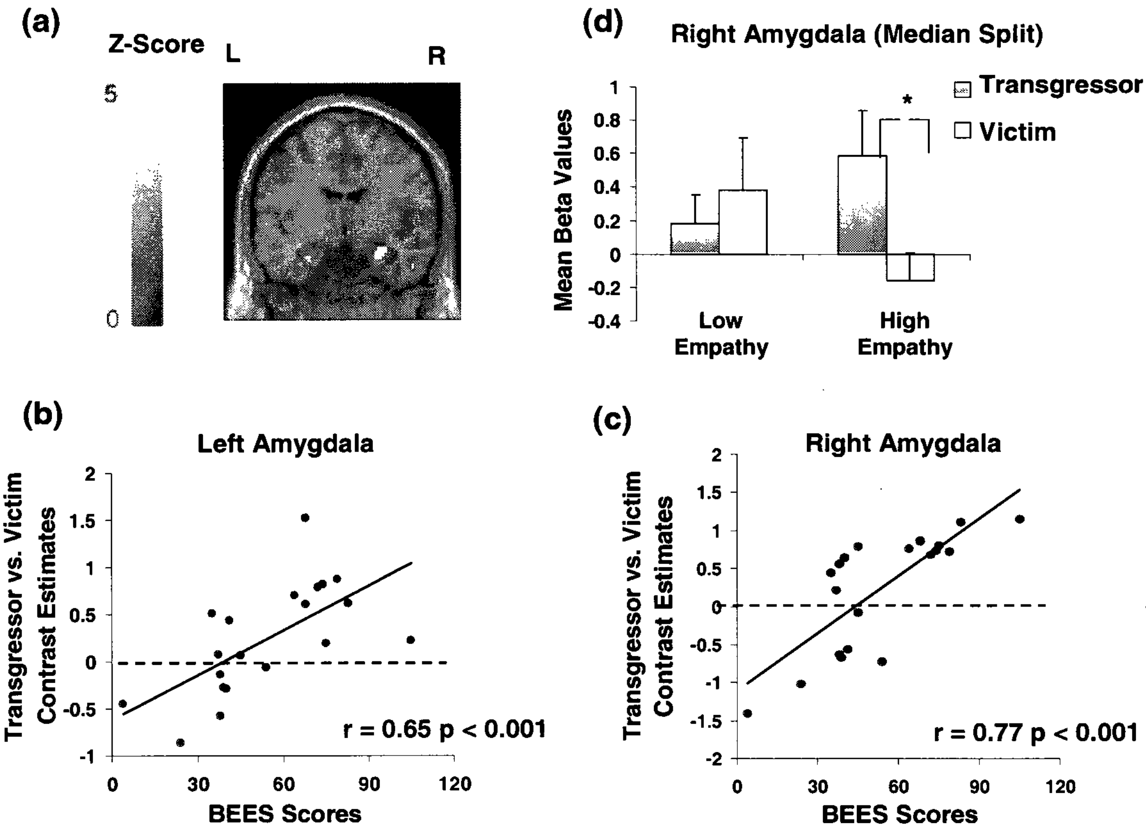


Figure 6: Trait empathy correlates positively with the left and right amygdala response to transgressors versus victims. (a) a whole brain correlational analysis yielded a significant clusters in the left (*xyz* = [-28,-10,-24], Z=3.72, 5 voxels) and right (*xyz*=[28,-8,-20], Z=5.26, 102 voxels) amygdala. (b) correlation between BEES scores and contrast estimates for transgressors versus victims in the peak voxel of left amygdala (c) correlation between BEES scores and contrast estimates for transgressors versus victims in the peak voxel of the right amygdala (d) median split into low and high trait empathy subgroups based on participants' BEES scores. Parameter estimates are plotted against their respective controls. Error bars represent the standard error of the mean. Parameter estimates for transgressors differed significantly from victims in the high trait empathy group ($p<0.005$), but not in the low trait empathy group ($p>0.4$). There was a trend towards a significant difference between the parameter estimate for transgressors and control person 1 in the high empathy subgroup ($p=0.06$). Parameter estimates for victims did not differ significantly from controls in both subgroups (ps>0.2). Parameter estimates for the two control persons did not differ significantly from each other (ps>0.8).

Figure 7

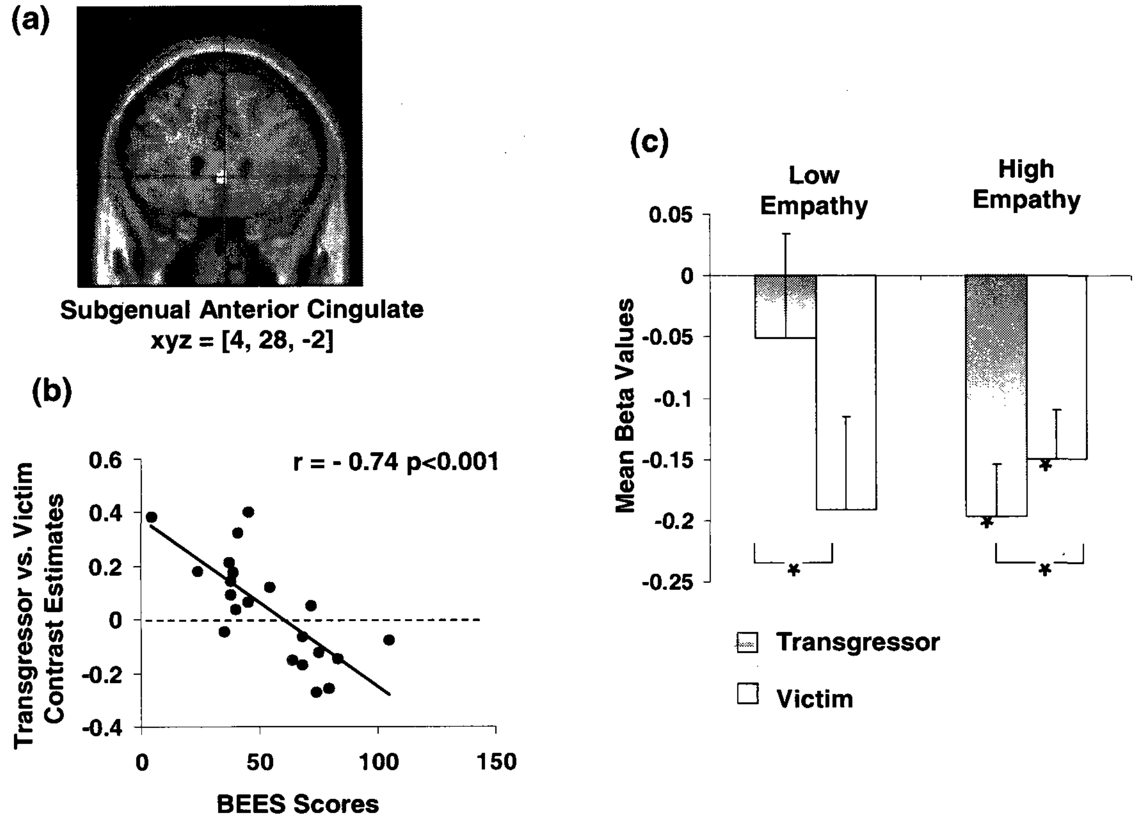


Figure 7: Trait empathy correlates negatively with the right subgenual anterior cingulate response to transgressors versus victims. (a) a whole brain correlational analysis between trait empathy scores (BEES Scores) and the contrast transgressors vs. victims yielded a significant cluster in the right subgenual anterior cinguate gyrus (*xyz*=[4,28,-2], Z=3.87) (b) a scatterplot displays the correlation between BEES scores and the peak voxel in the subgenual ACC. (c) Median split into 11 low empathic individuals and 10 high empathic individuals. Parameter estimates are plotted against their respective controls. Error bars represent the standard error of the mean. Low empathic individuals responded stronger to transgressors compared to victims ($t(10)=4.16$, $p<0.005$). Conversely, high empathic individuals responded stronger to victims ($t(9)=-2.80$, $p<0.05$). Parameter estimates for transgressors and victims differed significantly from their respective controls in high empathic individuals (*ps<0.01), but not in low empathic individuals (ps>0.06). Parameter estimates for control persons did not differ significantly from each other (ps>0.18).

Figure 8

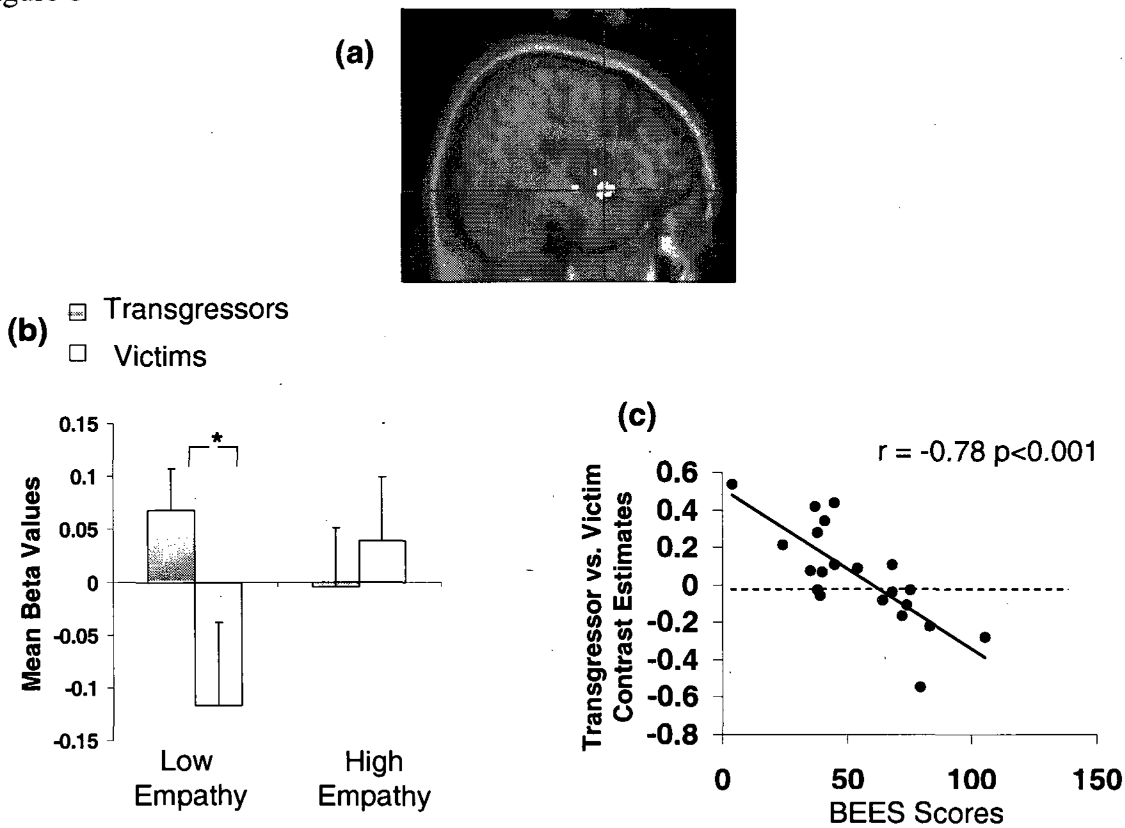


Figure 8: Trait empathy correlates negatively with the right anterior ventral insula response to transgressors versus victims. (a) a whole brain correlational analysis yielded a significant cluster in the right insula (*xyz* = [44,6,-12], Z=4.14). (b) Parameter estimates are plotted against their respective controls. Error bars represent the standard error of the mean. Low empathic individuals (median split) responded significantly stronger to transgressors relative to victims (t(10)=3.59, p=0.005). Responses of high empathic individuals towards transgressors did not differ significantly from victims (t(9)=-2.13, p=0.06). Parameter estimates for transgressors and victims did not differ significantly from their controls in both groups (ps>0.1). No significant differences between parameter estimates for control person 1 versus control person 2 were observed (ps>0.16) (c) a scatterplot depicts the correlation between BEES Scores and contrast estimates (*xyz* = [44,6,-12], Z=4.14) of the ventral insula response to transgressors versus victims.

Figure 9

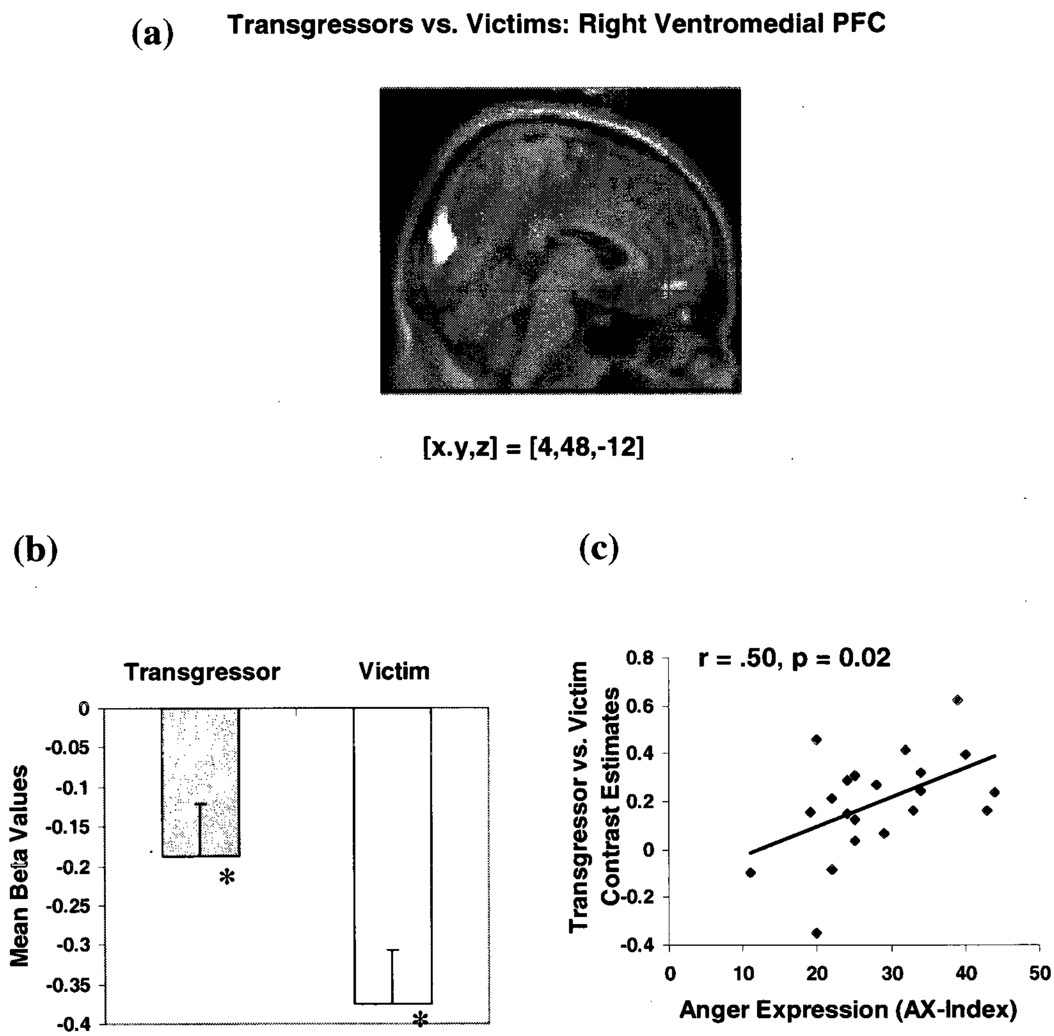


Figure 9: Anger Expression correlates positively with the vmPFC response to transgressors vs. victims (a) significant activation difference (p<0.001 uncorrected for multiple comparisons) for transgressors versus victims attended in the 5 second model in the vmPFC (b) parameter estimates for the peak voxel (*xyz*=[4,48,-12], Z=3.52) in the vmPFC response to transgressors versus victims are displayed. Parameter estimates for transgressors and victims are plotted against their respective controls. Error bars represent the standard error of the mean. Significant differences from zero (* p<0.05) indicate a significant difference between a parameter estimate and its respective control condition. Parameter estimates of the two control conditions did not differ significantly from each other in any peak voxel (all ps>0.7). (c) A scatterplot displays the contrast estimates for transgressors vs. victims attended in the ventromedial prefrontal cortex as a function of anger expression scores (AX-Index).

APPENDIX